AN INTRODUCTION

TO THE VERTEBRATES

BY

LEVERETT ALLEN ADAMS

Professor of Zoölogy, and

Curator of the Museum of Natural History

University of Illinois

SECOND EDITION

NEW YORK

JOHN WILEY & SONS, INC.

LONDON: CHAPMAN & HALL, LIMITED

PREFACE TO SECOND EDITION

In making a revision of the text, the writer wishes to express his appreciation to colleagues who have used the book, and have pointed out errors and means of improvement. The criticisms and suggestions, many of which have been incorporated in the new edition, have been very helpful.

I am especially indebted to Dr. B. V. Hall, Dr. Steggerda, Dr. Paul Beaver, and other colleagues, who have been of great assistance in the work of revision. The form is changed slightly, since the comparative anatomy section has been moved to follow the first section, thus transposing the original second section to the back of the book, where it can be studied or not, as desired. A number of illustrations have been added, others replaced, and some omitted. The section on comparative anatomy has been practically rewritten, especially those chapters that proved too short and too limited in material.

PREFACE TO FIRST EDITION

The plan of this introduction to the vertebrates is to provide, first, an outline of the characteristics on which the modern system of classification, of chordates is based; second, a general view of each of the five classes — fishes, amphibians, reptiles, birds, and mammals — with particular reference to representatives used in the laboratory; and, third, a comparative analysis of anatomical systems and specialized structures. This order of procedure has been followed during the last six years in the conduct of classes of students at the University of Illinois and is believed to be in harmony with the procedure in many other universities and colleges. It does not presuppose that the students begin with any previously acquired concepts of taxonomy, morphology, or paleontology, though they may have gained some advantage from a prerequisite course of study of the invertebrates and perhaps a preparatory course in biology. The success of this method of presentation is attested by the quickened interest of the students, by their progress in the work itself, and by the facility with which they enter upon subsequent work in embryology, osteology, and other fields of specialization. The degree of repetition necessitated by the plan of treatment may be considered as a factor in its success, rather than as an obstacle; for the students in coming upon a restatement of a fact usually find it in new relationships which are aids to memory and understanding.

Since the book is intended only as an introduction, no part of the subject matter is treated exhaustively. The chapter on classification, for example, should lead to an acquaintance with the standard works of authorities on each class of vertebrates, and the chapters on organs and systems should stimulate constant reference to the larger and more complete handbooks now available in English as well as those in German. Numerous supplementary details, of course, are to be discovered by the students in the dissection of specimens and pointed out by the instructor in lectures and discussions.

The illustrations, all of which are either new or redrawn, include many original drawings made by the writer over a long period of years — from hundreds of dissections — and selected for their value in demonstration. The small figures used in the chapter on classification were redrawn from many sources, most of which will be recognized. The schematic diagrams represent new arrangements of materials devised

after the prolonged use of many such diagrams in lecture and class work. The sources, where not obvious, are accredited in each case. The artistic merits of the illustrations are due to the skill of Mrs. Katharine H. Paul, Scientific Artist of the Department of Zoölogy at the University of Illinois, who has worked over the drawings, remaking some from the writer's sketches, smoothing others, and preparing all for the engravers.

The writer wishes to·express appreciation for suggestions and advice from his colleagues, particularly Dr. Waldo Shumway, Dr. Harley J. Van Cleave, Dr. Alvin R. Cahn, Dr. Frank B. Adamstone, and Dr. Orlando Park, each of whom read and criticized parts of the manuscript. Assistance in the arrangement of material and in the wording of the text was received from Mr. H. Carl Oesterling, Editor of the University of Illinois Press, who revised the manuscript and read the galley proofs.

I am much indebted to Dr. B. V. Hall for helpful suggestions and corrections in the fourth printing.

L. A. ADAMS

URBANA, ILLINOIS
April 15, 1933.

CONTENTS

PART ONE

PART TWO

PART THREE

PART ONE

AN INTRODUCTION TO THE VERTEBRATES

INTRODUCTION

Lamarck (1744–1829) made the first scientific division of the animal kingdom into two parts, calling one the Vertebrata and the other the Invertebrata. This is a very convenient division, and it is rather easy to place in one group all animals that have a vertebral column and in another group all that do not. Some of the invertebrates, such as the insects and certain snails, starfish, and sponges, have an exoskeleton, formed by cell secretions on the outside of the body, but not made up of specialized cell structures like the internal skeleton of the vertebrates. After the time of Lamarck there was discovered an intermediate group of small animals living in the sea which did not fit into his classification. They are related to the vertebrates but have a more simple structure. When it was found that this intermediate group, now known as the protochordates, had no vertebrae, it was necessary to make a new classification that would include all these related animals with the vertebrates. This new division, or phylum, was given the name *Chordata* by Balfour in 1880. The name Vertebrata was retained as a subphylum, and the lower forms, or protochordates, were divided into three other subphyla known as the Hemichordata, the Urochordata, and the Cephalochordata.

All members of the phylum Chordata have three characteristic structures: (1) an axial skeleton of some kind, (2) a series of pharyngeal gill slits, and (3) a tubular nervous system that is dorsal to the digestive tube. These three structures are present in some stage of the development of every chordate.

The primitive axial skeleton of the chordates is the *notochord*, an elastic rod that lies between the spinal cord and the digestive tube and usually extends from the head region to the tip of the tail, though it reaches only to the ear region in the embryos of vertebrates. It acts as a stiffening rod and gives the animal an advantage in the use of

the segmental muscles. Nothing similar is found in other phyla, although a strand of fibers in the annelid worms is sometimes compared with it, but with little justification. The axial skeleton of the vertebrates consists of the vertebral column and the skull.

The pharyngeal gill slits of the chordates are a series of paired openings that make their appearance at some time in the development of every member of the phylum, even in those forms that do not use them in adult life as accessories for breathing. Early in the evolution of chordates, as respiration could no longer be carried on through the skin alone, it became necessary to have some sort of openings through which water could reach the tissues that were specialized for the interchange of gases. In fishes and other water-living chordates the gill slits are the openings between the gill arches, and in animals that breathe with lungs the gill slits still appear at some stage of embryonic development.
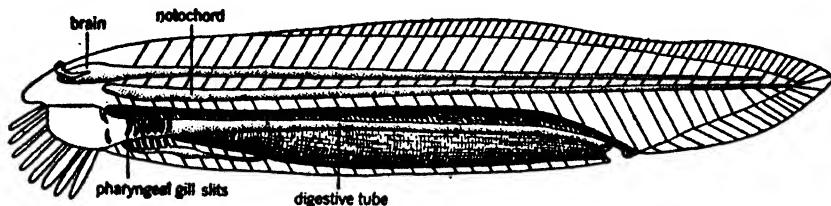

FIG. 1. Diagram showing the three principal characters of a chordate.

The central nervous system of the chordates is a tubular structure that is always dorsal to the notochord and the digestive tube. It originates from the outer germ layer, or ectoderm, in the embryo. It appears along the median line of the back, first as a narrow plate, then a groove, and finally a tube, which separates from the parent ectoderm and becomes the spinal cord; its anterior end is enlarged to form the brain. It thus differs from the nervous system of the invertebrates, in which the nerve cords are lateral or ventral and may be curved around the esophagus, forming an esophageal ring. The spinal cord and the brain maintain their dorsal position and their dominating relationships to other structures throughout the vertebrates.

Characteristics of Vertebrates

Besides the three primary characteristics, numerous other distinctive structures have appeared in the evolution of the vertebrates. Although the subphylum Vertebrata is a well-circumscribed group of animals, a very variable series of structures is to be expected when the environ-

mental conditions are examined, with water life on one hand and land life on the other. These two environments are very different, and each requires a number of anatomical and physiological adjustments. In a comparative study of the vertebrates, it is rather surprising to find how few entirely new structures appear between the fishes and the mammals, for almost invariably the finished structures of one class of vertebrates can be traced through earlier classes, where they can be seen in a simpler form, although they sometimes are performing an entirely different function. The first vertebrates lived in water, and their bodies were suited to this element; but as land vertebrates appeared there were striking changes in many structures and organs, since the anatomical and physiological needs were entirely different. In the first amphibians practically all the structures were present that were needed for land life, but they were comparatively simple for the most part. As the vertebrate scale was ascended the structures and organs generally kept pace with the new requirements, sometimes being better than were needed and sometimes rather inadequate. The improvements came about usually by minor adjustments of a structure already present, often by the addition of material borrowed from an entirely different source. Many of the vertebrate structures, however, are not represented at all in the invertebrates.

Bilateral Symmetry. — Vertebrates are bilaterally symmetrical, since a sagittal cut will divide the body into two equal halves, a right and a left. This bilaterality holds for all the main structures, such as the skeletal and nervous systems, and in general for the organs, although paired structures may not be exactly alike, either in size or in position. The liver, lungs, kidneys, and reproductive organs, though paired, are not always of the same size and may be somewhat shifted in position. Bilaterality is not an exclusive vertebrate character, since it is also found in some of the invertebrate phyla.

Metamerism. — Repetition of structures in a linear series is a vertebrate characteristic which occurs also in annelid worms, insects, and some other groups of invertebrates. The lower vertebrates are strongly segmented both externally and internally, but in the higher vertebrates there is a tendency for the external segmentation to be lost or to become unrecognizable. The internal metamerism, however, is retained and is clearly evident in the skeletal, nervous, circulatory, excretory, and other systems.

Divisions of the Body. — The body of a vertebrate always shows a tendency to divide into regions — a head, a trunk, and a tail — which are more or less plain and distinct and are adapted to separate kinds of activities. The anterior end of the body is always characterized by

the mouth, or entrance to the digestive tube, with accessory structures that aid in food-getting, such as the sense organs, jaws, and salivary glands. · Even in the lowest vertebrates there is some kind of a skull and jaws or a substitute.   Once started, this head region continues to develop, and the gradual centralization of the brain supplies the nervous material necessary for the sense organs.   The trunk region contains all the other organs, and they must adjust themselves to this cavity.   To protect them and to enable them to function, numerous developments have taken place in the skeletal parts.   In land animals there is a further differentiation of the trunk into a lumbar region and a sacral region.   The tail region is always post-anal, since the end of the digestive tube is not terminal.   The chief use of the tail is for locomotion.

The Skin and Exoskeleton. — The covering of the body of the vertebrates is quite different from that of the invertebrates, since it does not
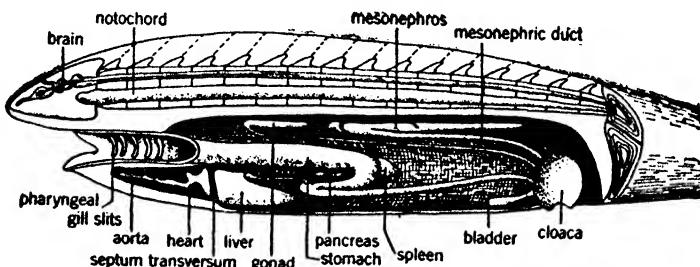

FIG. 2.   Diagram showing the organization of a vertebrate.   Redrawn from Wiedersheim.

develop any shell-like structures formed as cell secretions.   The skin of *Amphioxus*, a protochordate, is only one cell in thickness.   In vertebrates the epidermis, or outer layer of the skin, is made up of many layers of cells.   It supplies several kinds of structures, such as scales, feathers, hairs, horns, and glands.   The inner layer, or corium, is of mesodermal origin and contributes teeth, bony scales, abdominal ribs, and the dermal bones of the skeleton.   This layer is much more complicated in structure than the epidermis, for it contains blood vessels, nerves, connective tissue fibers, lymphatics, and other material.   It has made numerous contributions to the skeleton, for example, the teeth associated with the jaws and skull bones, the dermal scales or plates which finally become a part of the skull, and parts of the shoulder girdle, sternum, and fins.   Most of the vertebrates have specialized coverings.   Fishes with few exceptions have scales or plates, the ancient fishes having been supplied with a heavy armor, whereas in modern fishes there is a tendency for lighter scales of a different type.   The

amphibians of the present day are generally smooth and scaleless, but all their ancestral groups were scaled. The covering of modern reptiles is either scales or bony plates, though a few smooth forms appeared among ancient reptiles. Birds have scales on their feet and legs, and the feathers of birds are highly specialized structures that appear to have been derived from scales. Hair, the characteristic covering of mammals, is also probably associated with scales in its origin. It serves admirably in preserving a stable temperature and in protecting the body. Scales appear in some mammals, however, being found on the tails of many, on the feet, and often in embryonic development. A small order to which the pangolin belongs consists of animals entirely covered with large epidermal scales, and the group of American edentates, represented by the armadillo, has a covering of bony plates formed from the corium.

Endoskeleton. — The greatest advance made by the early chordates was in the development of the internal stiffening rod, the notochord, and the vertebrates have improved on this simple device by forming a complete inner skeleton of cartilage or bone that is far superior to anything to be found in the invertebrates. To support the weight of an animal with an outside skeleton requires an enormous amount of material compared to what is needed in an internal supporting system. No invertebrate living out of the supporting water has been able to reach any great size or weight. The largest invertebrates, those found in the Mollusca and the Arthropoda, though quite large, are supported by the water in which they live, and are utterly unable to adapt themselves to life on land. Some of the squids of the present reach a length of forty feet, some of the crustaceans of the past were six feet in length, and the extinct giant dragon flies had a wing spread of two feet; but the limit of size among the invertebrates generally is soon reached, and they can grow no larger. The insects are remarkable mechanically and have a proportionate strength far above vertebrates of the same size, but there is a definite limitation to the weight that they can support with their outside cuticular skeleton.

Skull. — The anterior end of the body in all vertebrates is supplied with some form of a brain case or skull. It is very simple in the lampreys and hagfishes, becomes a cartilaginous box in the sharks and their allies, develops through a number of intermediate stages, and finally attains the perfection of the skull of the higher vertebrates. The skull, in whatever stage it may be, is always in close correlation with the mouth, sense organs, and brain, protecting them or assisting in their functions. Originally cartilaginous as in the sharks, the skull became covered with a layer of protecting bone through the sinking in of dermal

plates, thus adding a series of elements to those that were to develop out of the cartilaginous chondrocranium. The history of the skull from the fishes to the mammals shows how this structure has kept pace with the stage of the animal, by adding new material, dropping out elements that were not essential, and changing the functions of some elements entirely. Superfluous elements associated with the gills of the fish, not needed in land life, were either dropped out or changed to fulfill a new rôle. The history of the ear and its bony structures reveals a number of interesting cases of change of function, whereby bones used in fishes for support were transformed so as to conduct sound waves to the inner ear.

Vertebral Column. — The original notochord of the lower chordates undergoes a series of changes in the vertebrates and is finally replaced by the vertebral column, although it still appears in the early developmental stages of every vertebrate (Fig. 3). This series of changes begins when mesodermal tissues are gradually condensed around the notochord, which serves somewhat as a core for them. At first these tissues are small semicircles; later they encircle the notochord as segmental rings, and eventually they develop into vertebrae. Thus the axial skeleton is changed from a continuous rod to a series of jointed units. The relation of these units to the original segments of the body is such that each completed vertebra lies in two segments, the anterior half in one and the posterior half in the next segment. The vertebrae, when fully formed, surround the notochord with a band which gradually pinches it out, either by constricting it or by sending spear-like processes into its substance, so that at last the notochord disappears entirely. The vertebrae become specialized in each region of the body and develop processes that hold them together although still permitting free movement. The ribs and sternum of the animals above the fishes make their appearance with land life; although ribs of two different types are present in the fishes, the sternum is strictly a structure of the amphibians and the higher classes of vertebrates.

Appendages. — The appendages of all vertebrates have a characteristic form and arrangement of parts. The limbs of amphibians, reptiles, birds, and mammals are comparable to the fins of fishes. The fins, though very variable, have a number of common characteristics, especially in position. On the sides of the body there are typically two pairs of fins, a pectoral pair near the head and a pelvic pair near the anus. Besides these paired fins, fishes have median fins derived from a single median structure that originally extended around the animal both dorsally and ventrally. This original continuous structure was modified by the specialization of the tail and by the elimination of

sections, so that separate dorsal and ventral fins were left. Pectoral and pelvic girdles began to develop early in the history of fishes, being attached to the body slightly at first as in the sharks but gradually acquiring a firmer connection. With the development of skeletal supports and the growth of muscles the possibility of movement becomes assured. The limbs of amphibians and higher vertebrates, in contrast to fins, are land structures primarily, and although probably derived from fins they are much better organized. Whatever changes may take place in them, the basic plan always remains the same. In land animals the pectoral girdle becomes firmly imbedded in muscle, while the pelvic
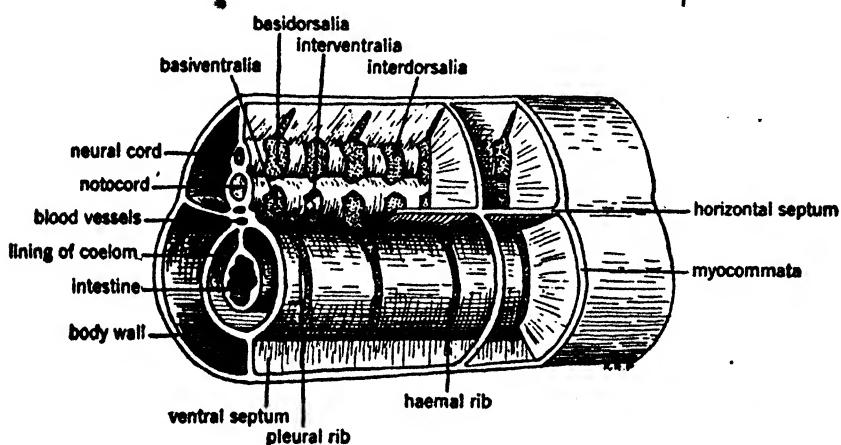
FIG. 3. Diagram of the developing body of a vertebrate, showing the relation of the septa, skeletal parts and coelom. After Goodrich.

girdle forms an attachment to the vertebral column. Water animals, with paddle-like limbs, still retain the tetrapod structure and not that of the fish fin.

Nervous System. — The nervous system of vertebrates is based upon centralization, with the brain and the spinal cord as the commanding parts. (Fig. 2.) It always originates in the same way, by the formation of a neural tube along the back of the embryo. The anterior end of this tube becomes the brain, and the nerve fibers grow out from the sensory ganglia and basal region to supply the sense organs with their necessary sensitive structures and to control the muscles in all parts of the body. As the vertebrate scale is ascended from fishes to mammals, there is more and more centralization in the brain, and with this centralization come added parts, increase in size, and better co-ordination. Thus the actions of the higher vertebrates become more and more under the control of brain centers, though numerous reflexes re-

main. The autonomic, or sympathetic, system is perhaps a strictly vertebrate characteristic, as nothing comparable to it is recognizable in the other chordates or in any other animals. It always plays an important part in the organization of the vertebrates.

Sense Organs. — Closely associated with the history of the brain are the sense organs, which always are connected with parts of the brain in which their centers are located. Some sense organs exhibit much more variation than others. The nose is always located at the anterior end of the animal and its variation is not great. The eyes, which are of a type different from anything found in the invertebrates, are stable throughout the vertebrate groups and vary little in principle from the lowest to the highest. The ears as organs of equilibrium are constructed on principles similar to those of the otocyst structures of the invertebrates. Their liquid-filled tubes, the semicircular canals, are supplied with sensory patches in which special cells extend their sensitive parts into the liquid; and any movement of the body causes the endolymph of these tubes to move, so that the calcareous otoliths, or "ear stones," touch the sensitive hairs. The sense of hearing starts with fishes, and is associated with definite sensory patches in the inner ear. The centers of equilibrium associated with the semicircular canals, and these centers of hearing, are in different parts of the brain. Taste and numerous other senses of lesser importance are common in the vertebrates, but most of these are modifications of the sense of touch and have rather simple anatomical structures.

Digestive System. — The digestive system consists essentially of a tube with an inlet, the mouth, and an outlet, the anus. Even in the lowest vertebrates the tube shows some differentiation of its parts, and in the fishes it has a number of distinct regions, always with a stomach and an intestine of one or more parts. In the higher vertebrates, as the body becomes more specialized, the digestive tube also becomes more complicated, with a strict division of labor in the complicated processes that it has to carry on. Two large glands, the liver and pancreas, are universal in the vertebrates (Fig. 2).

Coelomic Cavity. — The coelom, or mesodermal body cavity, becomes divided into two or three cavities in the vertebrates. The first limitation of the coelom is by the development of the septum transversum in the fishes, forming the pericardial cavity, which persists in the higher vertebrates. In mammals there is a further division of the coelom by the development of the muscular diaphragm, which encloses the lungs in a pleural cavity. The remaining cavity, containing the stomach, intestines, liver, kidneys, and other organs, is now called the peritoneal cavity. The coelom is lined with a mesodermic sheet

derived from the walls of the hypomere, while folds of this same material form the mesenteries which hold the organs in place, and supply the serosa which covers the intestines. (See Chapter XI for terms.) (Fig. 140.)

Respiration. — In contrast to the invertebrates with their varied means of respiration, this function in the vertebrates is localized in one region, the pharynx. In the early history of the chordates, when the body became large and the covering became rather impervious, some part had to become specialized for respiration. The mouth and throat region, being in close contact with the water, could do this with but little modification. The posterior end of the digestive tube was also available and is sometimes used for this purpose. The gills, with their lamellae or filaments, give the greatest exposure to the water, and the gill pouches and slits further increase the efficiency by permitting a steady stream to pass through them. Capillaries bring the blood near to the water in the gills so that exchange of gases is made easy. This is the system used in all fishes and in some amphibians. Any animal entirely dependent on such a system must die when changes in the water destroy the supply of oxygen. Therefore some other system had to be developed, and this began with the airsac, or air-bladder, a structure present in most fishes, which was used as a hydrostatic organ, sensitive to changes in pressure of the water, and assisted the fish to know the depth of the water. This airsac is an outgrowth from the pharynx as a rule, and it is used today by the lung-fishes and by a few others as an accessory organ for respiration. In land animals this structure probably became the main breathing organ, or lung, by completing the means of circulation of the blood already started in the fishes. With the advent of lung-breathing the gill slits tended to close, sometimes remaining open in the amphibians, but always closed in the higher animals which develop special breathing passages through the throat and nose (Fig. 2).

Circulation. — The circulation of the vertebrates is a closed system, and the haemoglobin is in special cells, the erythrocytes, which are new blood structures not found in the invertebrates. The forcing system is much improved and depends upon a definite muscular heart, which is a modified section of a blood vessel. In the animals above the protochordates the heart always has at least two-chambers, a receiving and a sending. In amphibians it is divided into three chambers; and finally in some reptiles, all birds, and all mammals it has four chambers, two receiving and two sending. Valves develop in the heart chambers to prevent any backflow of the blood, and all outgoing vessels from the heart are provided with semilunar valves, as also are the veins in all parts of the body. The blood itself does not diffuse through the tissues

of the body but is always confined in arteries, veins, or capillaries. The arteries have fairly thick walls; the veins have walls that are comparatively thin. The capillaries are extremely small and very thin-walled, permitting the escape of the plasma and the white corpuscles, so that these may come in direct contact with the cells. The blood vessels, being surrounded by a muscular sheet, are able to decrease or enlarge their caliber under control of the vasomotor nerve connections. The lymphatic system, always in close connection with the rest of the circulatory system, brings back into circulation the fluids that have escaped from the capillaries.

Excretion. — Excretion is carried on principally by structures that extract the waste materials gathered up in the circulation around the body. The kidneys, the primary organs in this work, are connected with the circulatory system, and a stream of blood is constantly passing through them. According to their structure and phylogeny, the kidneys fall into three types in the chordates: (1) the pronephros, the primitive kidney, loosely organized and found only in the protochordates and in embryonic development of the vertebrates; (2) the mesonephros, the kidney of the fishes and amphibians, which is much larger and much more effective in its work, because of its better mechanical arrangement and its improved and more numerous units of structure; and (3) the metanephros, the kidney of the reptiles, birds, and mammals, which is more compact and by its structure better suited for its function. The blood supply of the kidneys comes primarily from the arterial system, partially so in fishes and amphibians, and entirely so in birds and mammals, with the reptiles transitional. With each complete circuit of the blood around the body, a portion is led by arteries and capillaries into the structural units of the kidneys, and portions of the water, urea, uric acid, salts, and other wastes are able to get through the separating membranes of Bowman's capsule and into the tubules. The tubules are lined with cells which make a selection of the materials exposed to their walls, and thus return to the blood a part of the water and materials that are not waste. The renal portal system, typical of fishes and amphibians, conducts the venous blood from the posterior end of the body, winding around the tubules of the kidney units, and exposing the blood to these active cells. A urinary bladder may or may not be present (Fig. 2).

Reproduction. — Starting with the fishes, the chordates normally have separate sexes. The young are developed from fertilized eggs, which may be laid or may be retained in the body until hatched, or may be attached to the wall of the uterus by a placenta as in the highest mammals. The placenta serves as a structure through which food is

conducted through membranes, waste is returned to the mother for excretion, carbon dioxide is removed, and oxygen supplied. The genital organs and kidneys have parts in common, especially in the males of the higher vertebrates, where the same ducts may carry the products of both. Fertilization is generally external in water-dwelling vertebrates, and internal in the animals that are terrestrial.

The Problem of the Ancestry of the Vertebrates

The origin of the chordates seems to have been at a time comparatively late in the history of animal life, since they did not appear until all the invertebrate phyla had been differentiated. Most of the evidence of their ancestry has been lost, since the early chordates were soft-bodied, so that preservation of the critical parts was unlikely. Many theories have been proposed concerning the possible ancestral lines; but, since all the evidence so far is circumstantial, no one theory has been entirely satisfactory.

One of the earliest theories was that of Geoffroy St.-Hilaire (1807), who evidently spent a great deal of time speculating on the relationships of different animals and trying to make them all fit a common mold. His ideas are rather remarkable, since they came at a time long before any definite concept of evolution was formulated. He had made the discovery that the skulls of young animals were much better than those of old ones for the study of the separate elements of which they were composed, and he used them in making his comparisons. He decided that dorsal and ventral meant little, and to support this he cited animals that had changed their orientation, such as the back-swimming insects (*Notonecta*), the squids, and the flat fishes such as the halibut. He compared the chitinous rings of insects to vertebrae, compared the position of the viscera and exoskeleton of insects to the conditions found in the turtle with its shell, and considered that the legs of insects could be compared to the ribs of vertebrates. With the belief that all animals could be fitted to a common pattern, he conceived the idea that the insect, if turned on its back, could be made to agree with the conditions found in the vertebrates as he knew them then. Although this theory is interesting, it adds little to our knowledge of the origin of the chordates.

The nemertean worms were suggested by Hubrecht (1883) as possible ancestors of the early chordates. He assumed that the proboscis sheath could be compared to the notochord and that cephalic pits could be compared to gill slits. The lateral paired nerve cords, he thought, could have migrated dorsally to form a single cord comparable

BIRDS

Modern Birds NEORNITHES
  Flying
  Walking

Ancient Birds ARCHAEORNITHES*
  Archaeopteryx

MAMMALS

EUTHERIA Modern Placental
  Mammals

METATHERIA Pouched
  Animals
  Opossum
  Kangaroo

PROTOTHERIA Egg-layers
  Echidna
  Duckbill

REPTILES MAMMAL-LIKE REPTILES*
  Cynognathus*

DIAPSIDA PARAPSIDA
Pterodactyls* Snakes CHELONIA
Crocodiles Lizards Turtles
Dinosaurs* SYNAPSIDA

ANAPSIDA
  The Most Primitive Reptiles

AMPHIBIANS

  ANURA
Toads and Frogs

  URODELA
Tailed Amphibians

  GYMNOPHIONA
Worm-like
  Amphibians

  STEGOCEPHALIA*
Ancient Amphibia

FISHES

  DIPNOI TELEOSTEI
  Lung-fishes Modern
  Bony Fishes

  CHONDROSTEI
  Sturgeons
  Paddlefishes

CROSSOPTERYGII
  Lobe-finned HOLOSTEI
  Gars, Bowfin

  ELASMOBRANCHII
  Sharks, Rays, Chimaera

PROTOCHORDATES

  CYCLOSTOMATA
  Lampreys, Hagfishes

CEPHALOCHORDATA
Amphioxus OSTRACODERMATA*
  Primitive fish-like animals

  UROCHORDATA
Tunicates, Ascidians

  HEMICHORDATA
Balanoglossus

DIAGRAM 1. The phylogeny of the chordate classes.

to the central nervous system, leaving a pair of lateral nerves that would correspond to the lateral branches of the vagus nerve of the chordates. Though of some interest, this theory has received little attention, since there are few facts on which to base any such assumptions.

Patten, in his numerous papers, and in his books, the " Evolution of the Vertebrates and their Kin " (1912) and " The Grand Strategy of Evolution " (1920), presents a very ingenious theory to account for the origin of the chordates. He ignores the protochordates entirely as being specialized offshoots that lead nowhere. He maintains that *Amphioxus*, the tunicates, and *Balanoglossus* with its echinoderm affinities, were derived from an early invertebrate phylum and have no place in the phylogeny of the vertebrates. His ancestral line of the chordates is through the primitive arachnids such as *Limulus*, the primitive arthropod *Eurypterus*, and thence through the ostracoderms to the fishes. In comparing the arachnids and the chordates, he finds many points of similarity in the brain, heart, and aortic arches, and in the presence of gill pouches and external gills. Although many of the similarities are striking, there is the possibility that convergence and coincidence should receive more consideration. He states that the different parts fit together like a picture puzzle, and if one follows his writings and illustrations it certainly appears to be so. Recent discoveries of new beds of ostracoderms in Norway by Stensiö and Kiaer, and discoveries by Professor Patten himself on the island of Oesel, have made available material in a good state of preservation, the study of which lends itself to the strengthening of the Patten theory.

The most fantastic theory is that of Gaskell (1896), who attempts to derive the chordates from the arthropods by a series of structural and functional changes that are startling in their boldness. From his studies on arthropods and cyclostomes, he has come to the conclusion that the old digestive system of the arthropod became surrounded with nerve tissue and gave rise to the brain and spinal cord, and that the ancestral mouth is represented by the infundibulum of the chordate brain. He supposes that a new digestive system was formed from the ventral wall of the body by a similar process. Such alterations of function seem absurd, and to assume that they occurred does not make our problem any less difficult.

The annelids have been a favorite group in the search for chordate ancestry, and after the publication of Darwin's " Origin of Species " they were studied intensively by numerous workers: Dohrn, Semper, Delsman, and others. The attention of these students of phylogeny was attracted to the annelids because of several features that seemed to be comparable to chordate characteristics, including the segmenta-

tion of the body, the repetition of the urinary tubules (a condition found in the shark at about this time), the presence of a coelom, red blood, lateral locomotive organs, and a concentrated series of segments suggesting a head. It is now known that segmentation has occurred in numerous phyla and that it is not a fundamental character. The annelids offer no good evidence for the origin of gill slits, and although a structure called the " Faserstrang " has been compared to the notochord it is considered rather questionable. The " Faserstrang " is a string of cells that underlie the nerve cord and is enclosed with it in a common sheath. The annelid theory leaves too much to be explained, and its value must be determined largely by future discoveries.

The *Amphioxus* theory of Willey and others considers the protochordates as being in the line of evolution between the vertebrates and the hypothetical invertebrate phylum from which they branched off. Willey stresses the importance of the three fundamental characters of the chordates as found in *Amphioxus* and traces their ancestry to some worm-like form that was perhaps associated with the bilateral ancestors of the echinoderms. Thus the urochordates would be modified chordates related to *Amphioxus*, and *Balanoglossus* of the hemichordates would be a representative between the chordates and the echinoderms. Willey in his " Amphioxus and the Ancestry of the Vertebrates," says: " For the present we may conclude that the proximate ancestor of the vertebrates was a free-swimming animal intermediate in organization between the Ascidian tadpole and *Amphioxus*, possessing the dorsal mouth, hypophysis, and restricted notochord of the former, and the myotomes, coelomic epithelium, and straight alimentary canal of the latter. The ultimate or primordial ancestor of the vertebrates would, on the contrary, be a worm-like animal whose organization was approximately on a level with that of the bilateral ancestors of the Echinoderms."

Osborn in his " The Origin and Evolution of Life," 1917, says: " The double-pointed, fusiform body in which the segmented propelling muscles are external and a stiffening notochord is central, is the fish prototype, which more or less clearly survives in the existing lancelets (*Amphioxus*) and in the larval stages of the degenerate ascidians."

It seems probable that the chordates were derived from a line of ancestry that extended back in the geological periods, in fact back to the time of origin of most of the invertebrate phyla. The action of water currents on animals that were able to take advantage of the supply of food that could be obtained in the swifter waters would tend to place a premium on the development of an elongate fusiform body, with the segmented musculature necessary to propel it. Some type of

a stiffening rod, or other basis of muscle attachment, was necessary, aside from the development of intermuscular septa. One conclusion of this theory is that the ancestors of the fishes were derived from an early form of this *Amphioxus*-like stock, in which none of the specializations of the modern *Amphioxus* were present.

Chordates

At the foot of the chordate tree are three subphyla consisting of animals living at the present day that may show something of the ancestry of the vertebrates. Of course these modern forms cannot be considered as ancestral themselves, although their early representatives might have been. All these modern protochordates are small and live in the sea. Collectively they have three primary characters in common with the vertebrates: (1) an axial skeleton, (2) pharyngeal gill slits, and (3) a dorsal tubular nervous system. Some of these characters may disappear in the adults of the hemichordates and the urochordates, but all are retained in the cephalochordates. The brain is undifferentiated and, except in the cephalochordates, can hardly be called a brain at all. The sense organs do not appear or are poorly developed in the adult stage of these subphyla. The circulatory system, at its best, is rather incomplete, consisting of a simple tubular heart that is merely an enlarged blood vessel. (Fig. 1.)

Subphylum Hemichordata. — The hemichordates, represented by *Balanoglossus*, are small, acorn-headed, worm-like animals varying in length from a few inches to several feet. Their developmental history shows some characters that would point to a relationship with the Echinodermata, since the tornaria larva may be compared with the ciliated larva of the echinoderm group. They have pharyngeal gill slits which serve for respiration by bathing the blood vessels with water. A short diverticulum from the dorsal region of the digestive tube extends into the proboscis and stiffens it to aid in locomotion through the sand, and this is considered comparable to the notochord of the chordates. The nervous system develops in the same manner as in the chordates, from a dorsal longitudinal groove in the ectoderm, with some suggestion of a tubular structure; but in the adult there is a ventral as well as a dorsal cord. No excretory organs have been demonstrated, although ciliated pores open to the exterior from the region of the collar, connecting with a region in the proboscis that is richly supplied with blood vessels and may be compared to a glomerulus. The sexes are separate, the gonads opening to the exterior through the body wall (Fig. 4).

Subphylum Urochordata. — The urochordates are a large group of sea animals, consisting of both free-living and sessile forms. They are peculiar in that the young, or larvae, are typical chordates and are called tadpole larvae because of their resemblance to larval amphibians. The adults, whether free-swimming, sessile, or covered with cellulose tests, lose practically all their chordate characters and show much specialization and degeneracy. The notochord develops typically as in other chordates, but in adult life it practically disappears. The myotomic muscles in the tail region make it a vigorous propelling organ. The nervous system in the young is similar to that of other chordates, consisting of a tube expanded into a brain-like vesicle, an eye with a cuticular lens, and a calcareous mass representing the ear. These, however, remain only for a short period during development. A neuropore connects the brain vesicle with the exterior. In adult life the nerve structure is reduced to a small ganglion with anterior and posterior nerves and a smaller subneural ganglion which has a ciliated tubular connection with the pharynx, suggesting the hypophysis of the vertebrates. The pharynx is pierced by gill slits, usually two pairs in the young, but in the adults these are increased in number and strengthened and protected by a series of gill bars. In adults of the sessile forms the pharynx remains respiratory, and the rest of the digestive tube becomes an S-shaped structure with the anus near the mouth, its position being due to the covering of the animal by a test. The heart is tubular and directs the blood alternately forwards and backwards. The excretory system may consist of a series of vesicles placed close to the intestine, but without ducts. The reproductive system is of the hermaphroditic type, the ova and spermatozoa ripening at different times and passing through openings into the cloaca. The urochordates offer little that would help in solving the problem of the origin of the chordate stem, but they constitute a highly specialized and degenerate group with unquestioned affinities to the cephalochordates (Fig. 5).

Subphylum Cephalochordata. — The lancelets, represented by *Amphioxus* (*Branchiostoma*), consist of a small number of species and genera which are found along the coasts of many parts of the world, living near the shore and burrowing in the sand for protection. In parts of China they form a staple food at certain seasons of the year. They are chordates stripped of all but the bare essentials, and although they may supply interesting facts regarding chordate ancestry, they are modern forms and can hardly be looked upon as more than degenerate examples of a group that may have been an ancestral type. Their notochord, originating as a longitudinal dorsal ridge from the endoderm and ex-

tending from the nose to the tip of the tail, serves as a stiffening rod which with the myotomic muscles gives ample means of locomotion. The notochord is covered by two sheaths, the outer of which also covers the nerve cord. There are suggestions of skeletal material in other parts of the body; for example, in the oral hood there is a ring of a gelatinous material forming a delicate set of rods, with a series of rods extending into the cirri, and the pharyngeal region is also surrounded by a branchial basket formed of similar rods. The tail fin has a series of small supports formed by condensation of connective tissue. The nerve cord has a position typical of the chordates, being dorsal to the notochord and digestive systems. The brain, a slight enlargement of the nerve tube, is thin-walled and has an eye-spot between the first two cranial nerves. Its ventral diverticulum may be an infundibulum. In early development a neuropore opens from the neural canal. Segmented nerves arise from the cord, but the dorsal and ventral roots are unequal in number and do not unite as in vertebrates, nor do the nerves arise opposite to one another. It has been shown that the dorsal nerves carry motor as well as sensory fibers. The segmental nerves have no ganglia, and no autonomic system has been differentiated. The numerous gill slits, often numbering as many as fifty pairs, are supplied with cartilaginous bars which form a branchial basket suggesting that of the vertebrates. The clefts are covered by a fold of the body, the outlet being an atrial pore located considerably anterior to the anus. (Fig. 6.)

Subphylum Vertebrata. — Besides fishes, amphibians, reptiles, birds, and mammals, two lower classes — the ostracoderms and the cyclostomes — are included in the vertebrates.

Ostracoderms

The ostracoderms are the earliest known fish-like animals, and they seem to have some importance in chordate history. They appeared in the Ordovician period, reached their greatest expansion in the Silurian, and died out in the Devonian at about the time when the first amphibians were appearing. Little was known of their structure until recent fortunate discoveries supplied specimens in which their internal anatomy could be studied. Two genera, *Lasanius* and *Birkenia*, for years pictured upside down, have now been oriented in their proper position. The group varies from small tadpole forms, covered with denticles, to highly specialized animals, such as *Pterichthys*, with plates and scales and with peculiar appendages that cannot be compared to tetrapod limbs. The mouth appears to have been jawless

and of the sucking type. The ostracoderms would bridge a gap in the lower vertebrates and would be considered as being related to the cyclostomes (Fig. 7).

Cyclostomes

The cyclostomes are modern fish-like animals that appear to be remnants of an old fauna. They include two groups of partial parasites: (1) the lampreys, some of which attach themselves to the bodies of fishes, and (2) the hagfishes, which bore into the bodies of fishes and live in the interior until the carcass has been entirely stripped of flesh. The cyclostomes have some primitive characters, along with a number of specializations that seem to be a result of their parasitism. They differ from other vertebrates in having a single olfactory opening, no functional jaws, no paired fins, and a notochord with no constrictions, although small neural and haemal arches are present. *Petromyzon*, one of the lampreys (Fig. 8), is described below as characteristic of the cyclostomes.

The skeleton of *Petromyzon* consists of a notochord with two protective sheaths, an inner one and an outer one, as in *Amphioxus*; but there is an additional series of small imperfect neural arches which form a partial protection for the neural cord, suggesting the origin of vertebrae. The skull is a very simple structure, made up principally of the parachordals and trabeculae. At the anterior end is a primitive olfactory capsule, and the eye has a slight supporting arch, but the semicircular canals are surrounded by well-developed capsules which are joined laterally to the skull. Around the mouth are several cartilages that are difficult to interpret, in comparison with the higher vertebrate structures. The tongue is supported by a rather heavy lingual cartilage that has been suggested as representing the Meckelian cartilage of the higher forms. The pharynx is surrounded by a very complicated branchial basket, and its architecture is closely correlated with the peculiar action of the gill pouches, which do not function as those in fishes, since each cyclostome gill pouch, or sac, has its own musculature and an entirely different action. The median fins are supported by a number of small cartilaginous bars. The kidney is a simple mesonephros, but no nephrostomes are present. There is evidence of metamerism in the tubules of the kidney. No scales appear in any of the group. The teeth are of ectodermal origin and serve as rasping organs. The digestive tube is straight and shows little evidence of a separate stomach area; the liver and pancreas are represented only by follicles on the surface of the tube. No renal portal system is present. Respiration

is through a series of gill pouches, varying in number from six to fourteen. The nervous system of the cyclostomes is peculiar in several respects. The brain consists primarily of three lobes, the fore-, mid-, and hindbrain, with a slight differentiation of a cerebellum. Superficially the brain has some resemblance to that of *Necturus*. There are but eight cranial nerves, the others coming from the spinal region. Since there is a poor development of the sense organs, the optic lobes are small and inconspicuous. The eyes are small or rudimentary, and the auditory apparatus consists of two semicircular canals. The olfactory organ is peculiar in that it is continued posteriorly, ventral to the brain, forming a pituitary sac which corresponds to the hypophysis of the higher vertebrates. The spinal cord is much flattened; the spinal nerves are not formed by the union of dorsal and ventral roots as in the higher vertebrates, but instead the roots come off the spinal cord alternately. The circulatory system is somewhat fish-like, the heart having two chambers, an atrium and a ventricle. There is a separate respiratory tube, which opens into the pharynx, in contrast to the condition in fishes in which the gill slits open directly into the pharyngeal region (Fig. 8).

The *Ammocoetes* larvae of the lampreys are very interesting in their growth, because of the numerous ways in which they are different from the adults, and because of the numerous points in which they resemble the Cephalochordata. They do not have a sucking mouth, they have a brain that is larger proportionally than in the adults, and have a different arrangement of the median fin. Little is known of the history of the cyclostomes, since no fossils have been discovered that belong to this group. *Palaeospondylus gunni*, a small animal from the Red Sandstone of Scotland, is thought to be an early relative, but its relationship is conjectural. Most of the history must be inferred from the developmental studies of the *Ammocoetes* larvae.

Résumé

The vertebrates and the protochordates constitute one phylum, the Chordata. All chordates at some time in their existence have the following characteristics: an axial skeleton of some kind, pharyngeal gill slits, and a tubular central nervous system, dorsal to the digestive tube. Among other characters the vertebrates have developed the following: division of the body into a head, a trunk, and a tail; a highly developed endoskeleton; a cranium, composed of cartilage or bone; a vertebral column, which finally replaces the notochord; differentiation of the nervous system into a brain, a spinal cord, and a peripheral system; specialized sense organs of several kinds; a digestive system, including a liver and a pancreas; subdivision of the coelom;

respiration through gills or lungs, or both; a closed circulatory system, with haemoglobin in the erythrocytes; excretion by kidneys; sexual reproduction, with more or less difference between males and females. Among the theories concerning the origin of the chordates are: the insect theory of St. Hilaire; the arachnoid theory of Patten; the nemertean theory of Hubrecht; the annelid theory of Semper, Dohrn, Delsman, and others; the *Amphioxus* theory of Willey. The phylum Chordata is divided into four subphyla: the Hemichordata, Urochordata, Cephalochordata, and Vertebrata. The ostracoderms, a primitive group of fish-like animals that appeared in the Ordovician and died out in the Devonian, are usually placed below the fishes in the evolutionary scale. Some of them were tadpole-like, and others were covered with scales like fishes and had peculiar appendages not comparable to those of tetrapods. The cyclostomes, though somewhat similar to fishes, are below them in the evolutionary scale and are probably degenerate in many characteristics, such as the loss of fins, jaws, and scales. Ammocoetes larvae of lampreys are interesting because of their peculiar development.

THE GEOLOGICAL TIME SCALE. After Reeds and Lull.

		*		
PSYCHOZOIC	Recent	*	Rise of man	AGE OF MAN
	Pleistocene	1	Extinction of great mammals	
Cenozoic (Tertiary)	Pliocene	7	Origin of man	
	Miocene	19	Culmination of mammals	AGE OF MAMMALS
	Oligocene	35	Rise of higher mammals	
	Eocene	55	Disappearance of archaic mammals	
	Paleocene	60	Archaic mammals	
Mesozoic	Cretaceous	65	Highly specialized reptiles	AGE OF REPTILES
	Jurassic	35	Rise of birds	
	Triassic	35	Rise of dinosaurs	
Paleozoic	Permian	25	Rise of land vertebrates	AGE OF AMPHIBIANS
	Pennsylvanian	35	Rise of primitive reptiles	
	Mississippian	50	Rise of ancient sharks	
	Devonian	50	Rise of amphibians	AGE OF FISHES
	Silurian	40	Rise of lung-fishes	
	Ordovician	85	Rise of armored fishes	AGE OF HIGHER INVERTEBRATES
	Cambrian	70	First fishes?	
Proterozoic		650	Primitive invertebrates	
Archeozoic		650	Unicellulars	

* The figures in this column refer to estimates of the duration of these time periods, in millions of years.

CHAPTER II

CLASSIFICATION

Animals are classified for convenience, and their apparently formidable scientific names are really stenographic terms that save time and avoid confusion in identifying groups and species. Common names differ and may have only local currency, but the use of technical names makes it possible for scientific workers in all parts of the world to communicate their results. Before the days of the binomial system, a lengthy list of descriptive words was used, together with a common name, for designating a kind of animal, but of course this was so cumbersome and unsatisfactory that it could not readily be used in any scientific way. John Ray (1627–1705) is given the credit for having invented the binomial system of designation. By this system an animal has two names, a generic and a specific; for example, *Homo sapiens* is the scientific name for man. The system was used by Linnaeus and is now a standard way of naming all living things. For subdivisions, a third name may be applied, giving a distinction of varieties.

The long series of names used for the major and minor divisions of the vertebrates, as shown in the accompanying table, are merely convenient ways of indicating a number of forms united by a common set of characters. The characters of each group, though fixed arbitrarily, are supposed to express phylogenetic relationships. Any of these terms may be modified by a prefix, super- or sub-, to make them include more or less. The following list includes most of the terms now used in chordate classification:

Phylum	Chordata
Subphylum	Vertebrata
Superclass	Tetrapoda
Class	Mammalia
Subclass	Eutheria
Order	Carnivora
Suborder	Fissipedia
Family	Canidae
Genus	*Canis*
Species	*domesticus*
Variety	*albinus*

24

TABLE SHOWING CLASSIFICATION OF CHORDATES

Fossil forms are indicated by the asterisk(*)

Phylum Chordata.
- A. Subphylum Hemichordata.
- B. Subphylum Urochordata.
- C. Subphylum Cephalochordata.
- D. Subphylum Vertebrata.
  - I. Superclass Agnatha.
    - a. Class Ostracodermi.*
    - b. Class Cyclostomata.
  - II. Superclass Chondrichthyes.
    - a. Class Selachii.
    - b. Class Holocephali.
  - III. Superclass Osteichthyes.
    - a. Class Dipnoi.
    - b. Class Crossopterygii.
    - c. Class Actinopterygii.
      - i. Order Chondrostei.
      - ii. Order Holostei.
      - iii. Order Teleostei.
  - IV. Superclass Tetrapoda.
    - a. Class Amphibia.
      - 1. Subclass Stegocephali.*
      - 2. Subclass Euamphibia.
        - i. Order Gymnophiona.
        - ii. Order Urodela (Caudata).
        - iii. Order Anura (Salientia).
    - b. Class Reptilia.
      - 1. Subclass Anapsida.
        - i. Order Cotylosauria.*
      - 2. Subclass Synapsida.
        - i. Order Therapsida.*
        - ii. Order Chelonia.
      - 3. Subclass Parapsida.
        - i. Order Squamata.
          - a. Suborder Lacertilia.
          - b. Suborder Ophidia.
      - 4. Subclass Diapsida.
        - i. Order Dinosauria.*
          - a. Suborder Saurischia.*
          - b. Suborder Ornithischia.*
        - ii. Order Pterodactyla.
        - iii. Order Crocodilia.
        - iv. Order Rhynchocephalia.
    - c. Class Aves.
      - 1. Subclass Archaeornithes.
      - 2. Subclass Neornithes.
        - (a) Superorder Odontognathae.
        - (b) Superorder Palaeognathae.
        - (c) Superorder Neognathae.
    - d. Class Mammalia.
      - 1. Subclass Prototheria.
      - 2. Subclass Metatheria.
        - i. Order Marsupialia.
          - a. Suborder Polyprotodontia.
          - b. Suborder Caenolestoidea.
          - c. Suborder Diprodontia.
      - 3. Subclass Eutheria.
        - i. Order Insectivora.
        - ii. Order Chiroptera.
        - iii. Order Dermoptera.
        - iv. Order Philodota.
        - v. Order Xenarthra.
        - vi. Order Rodentia.
          - a. Suborder Simplicidentata.
          - b. Suborder Duplicidentata.
        - vii. Order Carnivora.
          - a. Suborder Fissipedia.
          - b. Suborder Pinnipedia.
        - viii. Order Cetacea.
        - ix. Order Hyracoidea.
        - x. Order Proboscidia.
        - xi. Order Sirenia.
        - xii. Order Artiodactyla.
        - xiii. Order Perissodactyla.
        - xiv. Order Tubulidentata.
        - xv. Order Primates.
          - a. Suborder Lemuroidea.
          - b. Suborder Tarsioidea.
          - c. Suborder Anthropoidea.

The history of classification shows the growth of the study of animals, since the early classifications, such as Aristotle's, were founded on a study of a small number of animals in a restricted region, whereas a modern classification includes the animals of the world, not only of the present but also of the past. Modifications have been necessary from time to time, as new animals were found. When *Ornithorhynchus*, Fig. 31, *Archaeopteryx*, Fig. 27, *Hesperornis*, Fig. 28, *Moa*, *Pithecanthropus*, *Amphioxus*, Fig. 6, and other striking forms were discovered, radical changes were made in classification, with additions of groups to include these different forms.

Probably the first classification was made by primitive man when he differentiated animals into those that were suitable to eat and those that were not. The ancient hunters divided animals into those found on land and those found in or around water. Some early attempts at scientific classifications were on this ground but proved unsatisfactory because they did not differentiate the fishes from the amphibians, the aquatic mammals, or other groups that make their homes in water. For many centuries the whale was called a fish. Aristotle used egg-laying as a means of separating animals, and though not a good measuring stick, it served very well for the time. Linnaeus took over most of the work of Aristotle without change, and thus continued this classification. John Ray used the blood as a means of separating the animals; and, since he had a much greater knowledge of anatomy at his command, he was able to work out some very significant improvements on the work of those who preceded him. Richard Owen based his classification on the form of the brain. The great impetus given to classification by Darwin's " Origin of Species " (1859) completely changed the trend, and from then to the present time classification has had a very different meaning. Instead of few external characters, the whole animal is now used, and with a greater knowledge of anatomy the grouping has been placed on a much sounder basis. Superficial resemblances and convergent forms have been separated and have been placed more nearly in their proper relationships. With evolution and phylogeny as central ideas, the study of classification has been assisted by many phases of zoölogy, such as anatomy, embryology, paleontology, geographical distribution, and, in more modern times, physiology and genetics — each of which has contributed to make the lines of differentiation more exact. Classification probably will never be fixed or static, but must change with additional knowledge that makes more certain the relationships of animals, both those now living and those that are extinct.

The following classification will give a general outline of the arrangement of the chordate groups with a brief summary of the characters of each division and subdivision.

Summary of Characters of the Groups and Subdivisions of the Chordata

PHYLUM CHORDATA. Bilaterally symmetrical; notochord and pharyngeal gill slits present at some stage of development; nervous system dorsal to the digestive tube.

I. Subphylum **Hemichordata.** Body worm-like with collar and proboscis; notochord in anterior part of body only; large, number of paired gill slits; resemble echinoderm larvae in development and are supposed to have echinoderm affinities. Examples: (Fig. 4) *Balanoglossus, Cephalodiscus.*

FIG. 4.   Balanoglossus.

II. Subphylum **Urochordata.** Adults quite different from larvae; body of sessile forms enclosed in cellulose mantle; gill slits and endostyle present in pharynx; a heart; sense organs in larvae. Examples: (Fig. 5) Tunicata, *Salpa, Appendicularia.*

III. Subphylum **Cephalochordata.** Small lancet-shaped animals living along the seashore. Head not well defined; notochord extends from tip of nose to tail; heart one-chambered and tubular; no paired appendages; no cranium; no blood corpuscles; gills in peribranchial chamber; epidermis but one cell in thickness. Examples: (Fig. 6) *Amphioxus (Branchiostoma).*
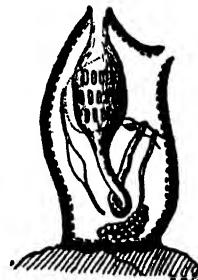
FIG. 5.   An Ascidian.

FIG. 6.   Amphioxus.

IV. Subphylum **Vertebrata.** Definite head, skull, and sense organs; red blood, circulation a closed system; heart of at least two chambers; brain complex and divided into definite regions; nephridial tubes usually carry away sex products; notochord reaches only to the ear region; vertebral column in some stage of development; few with larval development.

A. Superclass **AGNATHA.** Animals in which there is a sucking mouth and no jaws; brain in a simple stage.

Class *Ostracodermi.* Primitive fish-like forms, found in the Silurian and Devonian; usually with armored bodies; apparently no jaws; no paired appendages comparable to those of true fishes; mouth of sucking type; brain appears to have been rather complex. (Fig. 7) *Lasanius, Thelodus, Birkenia, Pteraspis.*

Thelodus   Lasanius   Drepanaspis
Birkenia   Pterichthys
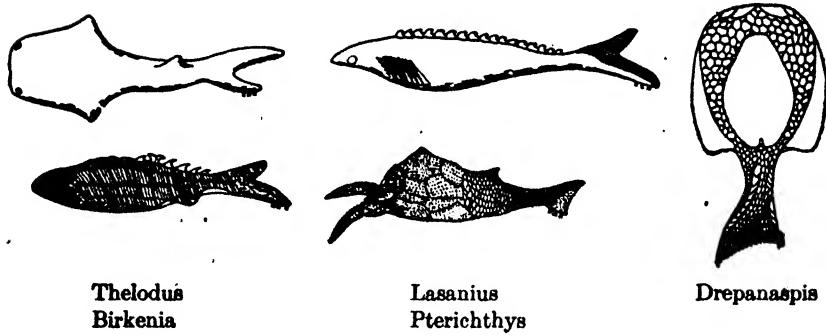
Fig. 7

Class *Cyclostomata.* Probably a degenerate group; mouth of sucking type, no jaws; skull primitive; brain three-lobed; sense organs present generally; nasal openings unpaired; heart of two chambers; lateral line present; no lateral appendages, salt and fresh water. (Fig. 8) *Petromyzon* (lamprey), *Myxine* (hagfish), *Bdellostoma* (hagfishes).

Lamprey   Hagfish
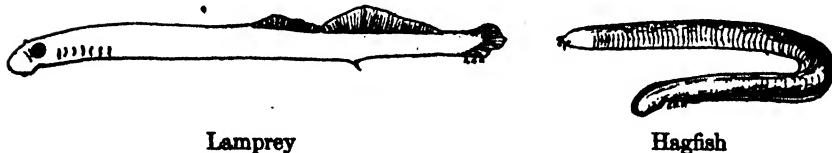
Fig. 8

Superclass **CHONDRICHTHYES.** Cartilaginous skeleton; true bone never developed; covered with placoid scales; jaws consisting of Meckel's cartilage and palato-quadrate; spiral valve in intestine; gill slits five to seven; tail heterocercal; no swimbladder.

Class *Selachii.* Chondrichthyes with no operculum over the gill slits. (Fig. 9) Elasmobranchii (sharks); Rajiformes (rays). Jaw suspension hyostylic.

Shark   Ray
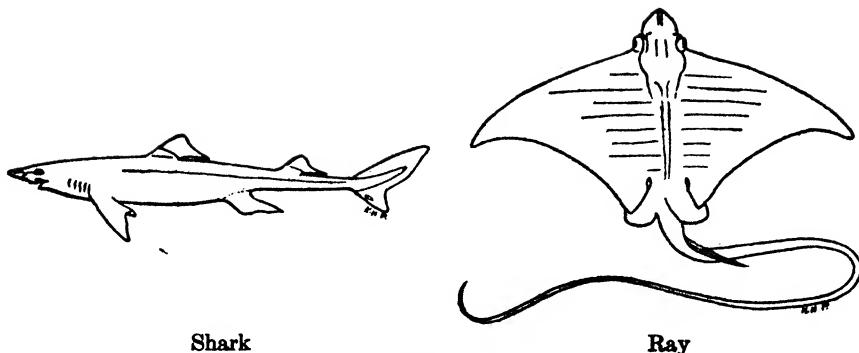
FIG. 9

Class *Holocephalia.* Chondrichthyes with an operculum
over the gill slits; a single narial opening; jaw suspension
autostylic. (Fig. 10) *Chimaera.*
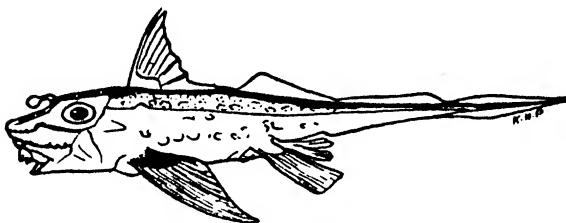
FIG. 10. Chimaera.

Superclass OSTEICHTHYES. Skeleton more or less bony; skin
usually covered with bony plates or scales; jaws consist of
Meckel's cartilage covered with a bony sheath; swim-bladder
present; dermocranium covering the chondrocranium and
forming the roof of the skull; dermal rays formed from scales;
pectoral skeleton with dermal bones.

Class *Dipnoi.* Lung-fishes; cranium largely cartilaginous;
dermal bones on median line of skull roof, not paired; no
pineal foramen; jaw suspension autostylic; vertebrae
acentrous; highly special dental plates instead of teeth;
scales cycloid; spiral valve in intestine; air-bladder alveo-
lated and used as a lung; atrium of heart partially divided;
sixth aortic arch used as a pulmonary artery; fins lobate
with rays biserial on a central axis. (Fig. 11) *Neoceratodus*
(in Australia), *Protopterus* (in Africa), *Lepidosiren* (in
South America).

Neoceratodus   Protopterus   Lepidosiren
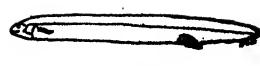
FIG. 11

Class *Crossopterygii*. Lobate fins with scaled bases; skeleton well ossified; scales rhomboid or cycloid; notochord constricted; teeth simple; gular plates between jaws; persistent spiracle; spiral valve in intestine; dorsal and ventral ribs; air-bladder alveolated and used as a lung. (Fig. 12) *Polypterus* and *Calamoichthyes* (in Africa). See page 47.
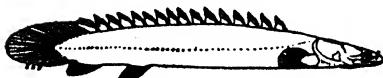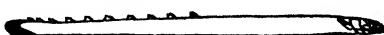
Polypterus   Calamoichthys

FIG. 12

Class *Actinopterygii*. Paired fins non-lobate; gular plates changed to branchiostegal rays; web of fins supported by dermotrichia; scales, of ganoid, cycloid, or ctenoid type; no cloaca.

    Order *Chondrostei*. Dermal skull well ossified; chondral skull not ossified; endoskeleton mostly cartilaginous; scales rhomboid or cycloid if present;
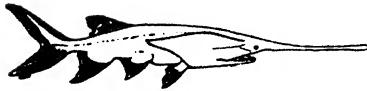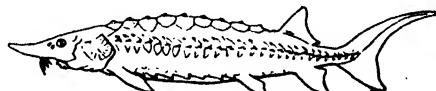
Polyodon   Acipenser

FIG. 13

spiracle present; tail heterocercal; air-bladder dorsal and unpaired; notochord little constricted by vertebrae; spiral valve in intestine. (Fig. 13) *Acipenser* (sturgeon), *Polyodon* (spoonbill), *Psephurus* (in China). Order *Holostei*. Both dermal and chondral elements well ossified; mouth terminal; notochord more constricted; tail typically heterocercal, but sometimes gephryocercal; air-bladder alveolar with large opening to esophagus and used in respiration; scales ganoid or

cycloid; no spiracle; spiral valve present in intestine. (Fig. 14) *Lepisosteus, Amia.*

Amia   Gar
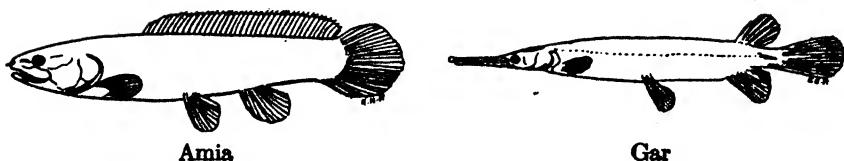
FIG. 14

Order *Teleostei.* Highest specialized fishes, with cranial elements well knit together; tail typically homocercal; scales cycloid or ctenoid; vertebrae amphicoelous; nephridial ducts do not form sex ducts; air-bladder not alveolar and either open to the esophagus (Physostomi) or permanently closed (Physoclysti); no spiral valve; well-developed opercular series of bones. (Fig. 15) Teleost.
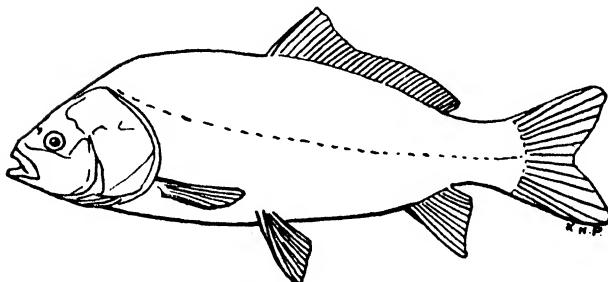
FIG. 15.   Teleost.

Superclass **TETRAPODA**.   Animals with definite limbs instead of fins; hands and feet typically constructed on a plan of five digits; skull greatly simplified by reduction or loss of bones originally used for the support of gills; stapes developed in newly acquired middle ear; girdles assume form capable of bearing weight on land; lungs highly developed with accessory structures beginning to function; body may be subdivided into at least three subdivisions, neck, trunk, and tail; body covered with scales, plates, hairs, or feathers, or naked.

Class *Amphibia.*   Tetrapods with a metamorphosis; capable of living in water as well as on land, at least in young stages; reduced visceral skeleton; two condyles on skull; three-chambered heart; ectodermal gills permanent in some; eggs

usually laid in water or damp places; generally no claws on digits; no salt-water forms.

Subclass STEGOCEPHALIA. Extinct amphibians (lower Mississippian to Triassic) at the base of the phylogenetic stem; head covered with bony plates (sculpturing shows that they were on surface); body generally scaled or plated; pineal foramen present; shoulder girdle fish-like with the cleithrum retained; vertebrae variable and peculiar; abdominal ribs present; (Fig. 16) *Eryops*, *Branchiosaurus*, *Loxomma*, labyrinthodonts.

Eryops   Cacops

Fɪɢ. 16

Subclass EUAMPHIBIA. Modern amphibians; not covered with plates or scales; no pineal foramen.

Order *Gymnophiona*. Small tropical snake-like amphibians, extending in a belt around the world, close to the equator; limbs lost; eyes reduced or absent; skull superficially like stegocephalian type; scales imbedded in the skin. (Fig. 17) *Ichthyophis*, *Herpeles*, *Siphonops*.
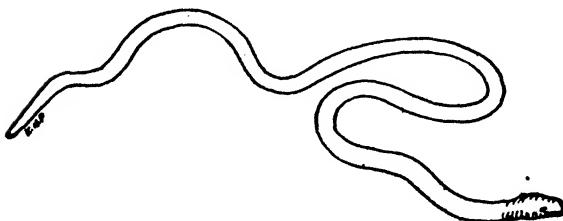
Fɪɢ. 17. Caecilia.

Order *Urodela*. Modern amphibians with tails; sternum primitive; gills retained or lost; girdles primitive; live in water and on land; (Fig. 18) *Necturus*, salamanders, newts, *Amphiuma*, *Siren*, etc.

Order *Anura.* Modern amphibians without tails except in larval stages; sternum and girdles highly specialized; visceral skeleton reduced; skin somewhat hardened in toads, but alive and glandular in frogs; specialization of the vertebrae, pelvic girdle, and limbs for locomotion. (Fig. 19) *Bufo* (toads), *Rana* (frogs).

Siren
Ambystoma

Amphiuma
Necturus
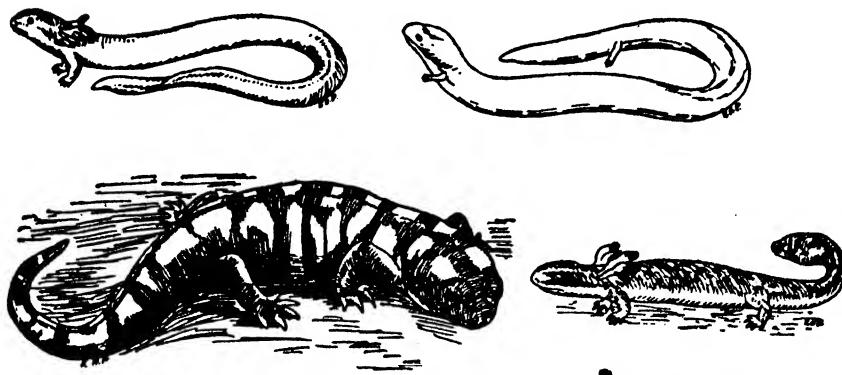
Fig. 18

Fig. 19. Rana.

Class *Reptilia.* Tetrapods without a metamorphosis; skin covered with a dead epidermal layer; usually covered with scales or plates; allantois and amnion present; eggs never laid in water; reproduction oviparous or ovoviviparous; parasphenoid of skull reduced or lost; single occipital condyle; sclerotic bones around eyeball; pineal foramen usually present; sternum highly developed; body usually made up of five regions; cerebral lobes increased in size and importance; lateral line lost.

Subclass **ANAPSIDA.** Primitive extinct reptiles (Permian to Triassic) in which the skull is completely roofed over.

Order *Cotylosauria.* Primitive extinct reptiles (Lower Pennsylvanian and Triassic) closely resembling the

stegocephalians. (This is the stem group of the reptiles.) (Fig. 20. Diadectes.)
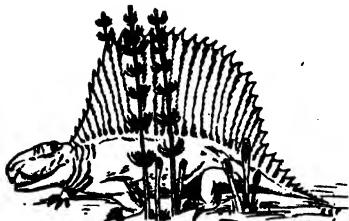
Dimetrodon

Fig. 20

Diadectes

Subclass **SYNAPSIDA.** Extinct reptiles of the Permian and Triassic, with a single pair of temporal openings in skull; which is primarily ventral to the postorbito-squamosal arch. (It is from this group that the mammals have been derived.) (Fig. 20. Dimetrodon.)

Order *Therapsida.* Extinct reptiles in which the posterior bones of the mandible and the quadrate are greatly reduced; teeth may be divided into incisors, canines, premolars, and molars. (Fig. 21) *Cynognathus.*
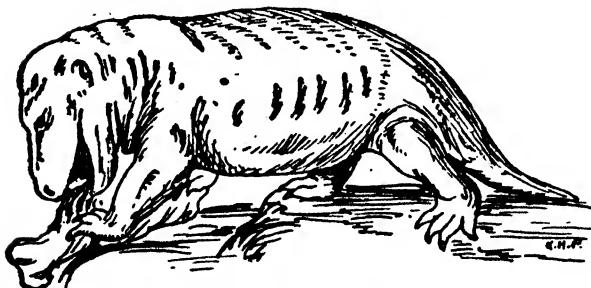
Fig. 21. Cynognathus.

Order *Chelonia.* Reptiles with a highly specialized skeleton, forming a carapace and plastron; usually covered with epidermal plates; vertebrae very variable; habitat on land, in fresh water, and salt water; skull resembles secondarily those of the lowest reptiles; jaws encased in horny shields, without teeth. Snapping turtles, soft-shelled turtles, box turtles, sea-turtles, etc.

Subclass **PARAPSIDA.** Reptiles with a temporal opening above the postorbito-squamosal arch.

Order *Squamata.* Body covered with scales or plates; ribs with single heads; no abdominal ribs; with quadrate movable; the modern forms may be divided into two suborders: (Fig. 22) Lacertilia, or lizards, and Ophidia, or snakes.

FIG. 22. Ring-necked lizard.

Subclass **DIAPSIDA.** Reptiles with two temporal openings separated by the postorbito-squamosal arch. (Early forms ancestral to the Crocodilia, Dinosauria, and Pterodactyla were probably ancestral also to the birds.)

| Camarasaurus | Triceratops | Allosaurus |
| Tyrannosaurus | | Allosaurus |
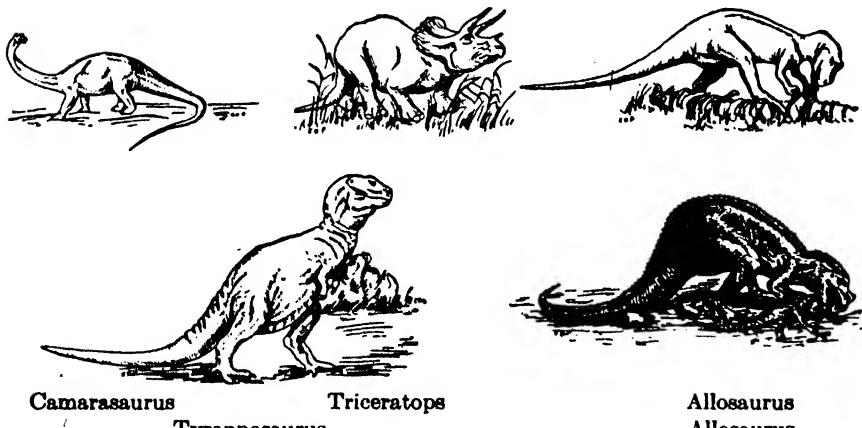
FIG. 23

Order *Dinosauria.* Fossil reptiles (Triassic to Upper Cretaceous), consisting of two great divisions, the Saurischia and the Ornithischia; the largest, most grotesque, and most variable of all the reptiles. Examples (Fig. 23) *Brontosaurus,* * *Iguanodon,* * *Diplodocus.* *

Order *Pterodactyla*. Flying reptiles of the Cretaceous period; hand modified for flying by elongation of the fifth digit; bones pneumatic. (Fig. 24) *Pteranodon.*
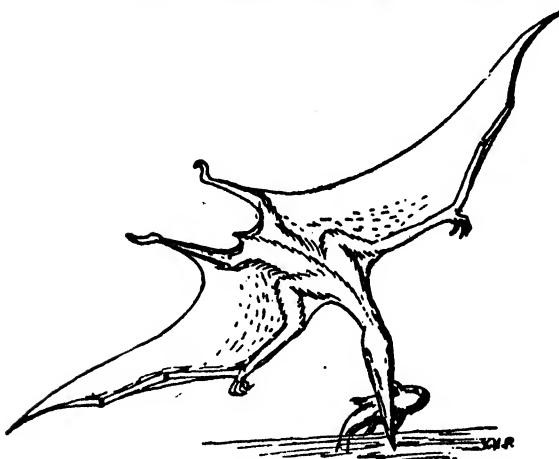
Fig. 24.   Pterodactyl.

Order *Crocodilia*. Reptiles with a four-chambered heart; abdominal ribs; life in the water; thecodont teeth; secondary palate driving the posterior nares to the pharynx; no pineal opening. (Fig. 25) Alligator, crocodiles, gavials, caiman, etc.
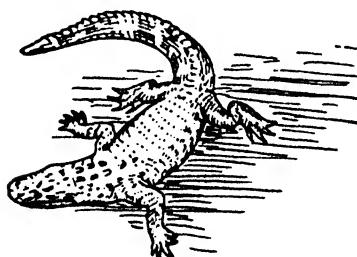
Fig. 25.   Alligator.

Order *Rhynchocephalia*. Reptiles with two arches in the skull, well-developed pineal eye, acrodont dentition; abdominal ribs present; reptiles represented by one modern species found in New Zealand: (Fig. 26) *Sphenodon punctatum* (common name sphenodon or tuatera).

Fig. 26.   Sphenodon.

Class *Aves*. Feathered bipeds; generally homothermous; heart four-chambered; right aortic arch only, left lost; modified fore limb specialized for flying; bones pneumatic in flying types; toes four or less; reproduction oviparous; single condyle to skull; quadrate free; tarsal bones combined with tibia and metatarsals thus forming an intertarsal joint; a long ilium; ancient forms with teeth, but modern forms with jaws encased in epidermal, horny sheaths.

Subclass ARCHAEORNITHES. The most primitive known birds, in the Jurassic period; skeleton reptile-like; verte-
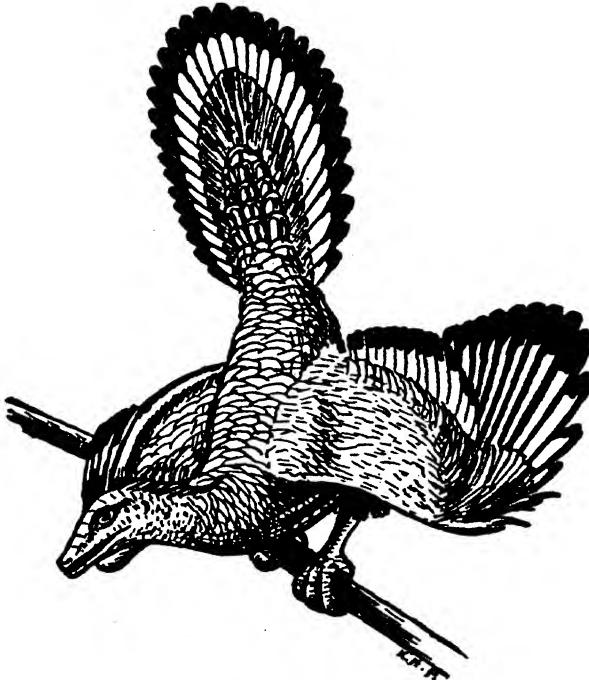
FIG. 27. Archaeopteryx.

brae amphicoelous; tail long, with a pair of feathers on each of its vertebra; sternum small or rudimentary; ribs needle-like, with no uncinate processes; fore limbs modified as wings, but with three clawed digits free; neck ribs present and free. (Fig. 27) *Archaeopteryx* and *Archaeornis*.

Subclass NEORNITHES. Tail vertebrae reduced and compressed, with arrangement of feathers; sternum well developed; ribs with uncinate processes; neck ribs joined to vertebrae.

Superorder *ODONTOGNATHAE*. Ancient toothed birds from the Cretaceous period; sternum keeled or flat. (Fig. 28) *Hesperornis regalis*,* *Ichthyornis dispar*.*

Superorder *PALAEOGNATHAE*. Walking birds, flightless; many of large size; sternum flat; wings rudimentary; coracoid and scapula small and ankylosed; tail vertebrae free; no furcula; feathers usually hair-like. Examples: (Fig. 29) ostriches, rheas, cassowaries, *Tinamus*, *Apteryx*, *Moas*,* and *Aepyornis*.*

Fig. 28. Hesperornis.
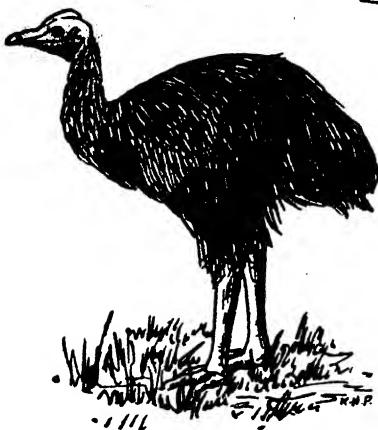
Cassowary

Apteryx

Fig. 29

Superorder *NEOGNATHAE*. Modern birds with a keeled sternum (that is, all modern birds not in the Palaegnathae); tail vertebrae five or six; fore limb with metacarpals joined and fingers included in the specialized wing; tarsometatarsus and carpometacarpus completely formed. (Fig. 30.)

Class *Mammalia*. Tetrapods with mammary glands, which supply milk to young; generally homothermous; three ossicles in ear; heart four-chambered; left aortic arch only, right lost; body covered with hair (sometimes with scales or bony plates); sweat and oil glands in skin; skull with two condyles; dentition heterodont; amnion and allantois in development; complete diaphragm; mandibles formed by

the dentaries only; blood corpuscles minute and non-nucleate; cervicals usually seven; eggs minute except in monotremes.
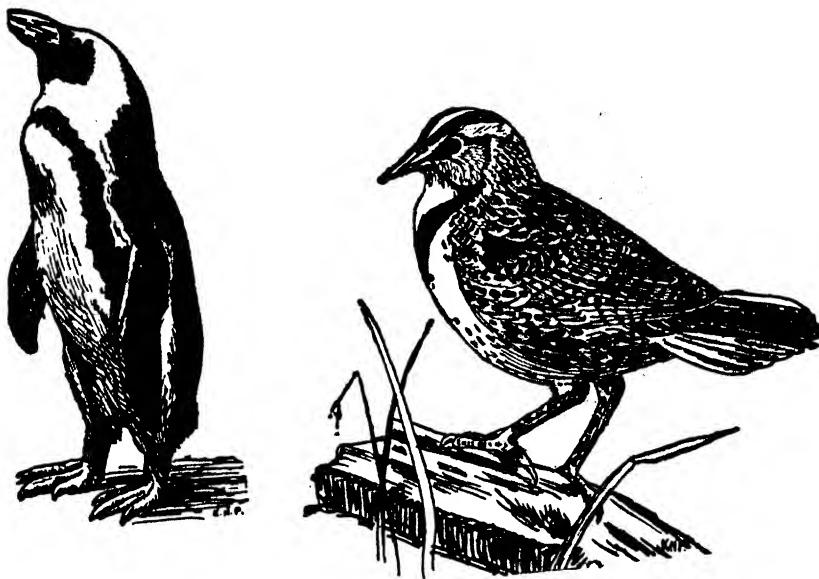
Penguin   Meadowlark
Fig. 30

Subclass **PROTOTHERIA**. Egg-laying mammals; mammary glands without teats; temperature variable; no placenta shoulder with coracoid, precoracoid, and interclavicle; epipubic bones present, scapulae without crests, brain of low type; cloaca. Examples: (Fig. 31) *Ornithorhynchus* (duckbill), and *Echidna* (spiny anteater), found in Australia and surrounding islands only.
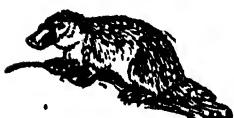
Duckbill   Spiny Anteater
Fig. 31

Subclass **METATHERIA**. Viviparous mammals; generally without a functional placenta; young born in immature stage; usually with a marsupial pouch and marsupial bones; nipples developed to which the young grow while

in the pouch; vagina often with a third diverticulum; palate usually fenestrated; angle of jaw inflected; distinct dental formula; brain of low type.

Order *Marsupialia.*
Suborder Polyprotodontia.   Opossum, native cats, etc.
Suborder Caenolestoidea.   *Caenolestes.*
Suborder Diprodontia.   (Fig. 32) Kangaroos, phalangers, etc.

Opossum   Kangaroo   Tasmanian wolf
Fig. 32

Subclass EUTHERIA.   Mammals with a functional placenta; brain case comparatively large; brain with corpus callosum; typical dental formula $\frac{3-1-4-3}{3-1-4-3}$; no epipubic bones; young highly developed when born.

Order *Insectivora.*   Usually small mammals with five digits all clawed; feet plantigrade; generally insect-eaters; teeth with many sharp points; canines slightly separated from incisors and premolars; brain small, with smooth hemispheres.   Examples: (Fig. 33) shrews and moles, cosmopolitan.

Shrew   Mole
Fig. 33

Order *Chiroptera.* Small mammals with fore limbs modified for flight; insectivorous and herbivorous; large olecranon process; five digits with claws; tympanic ring formed. Examples: (Fig. 34) Bats, all over the world.

FIG. 34. Bat.

Order *Dermoptera.* Small, clawed mammals with a fold of skin between the legs which acts as a parachute; herbivorous; pectoral teats; molars multicuspidate; peculiar comb-like lower incisors. Examples: (Fig. 35) *Galeopithecus* (flying lemur).

FIG. 35. Galeopithecus.

Order *Philodota.* Medium-sized, clawed mammals covered with large epidermal scales and but few hairs; toothless; tongue worm-like; feet plantigrade. Examples: (Fig. 36) *Manis*, pangolin.

Order *Xenarthra.* Large group of much-diversified edentates; tree-living, digging, and insectivorous; unguiculate; teeth, if present, are all of the simple

peg-like type, without enamel and rootless; skin covered with hair, horny or bony scales; thoracic and lumbar vertebrae with extra accessory processes.

FIG. 36.   Manis.

Examples: (Fig. 37) *Armadillo*, sloth, anteaters, *Megatherium.* An enormous group in past times, during the Miocene period in South America.

Order *Rodentia.* Clawed mammals, usually of small size, with incisors specialized for gnawing; feet plantigrade or semiplantigrade; usually herbivorous but sometimes omnivorous; incisors shaped like a half circle, with open roots and a persistent growth; no canines; wide diastema, or space, between incisors and molar series; molars with a distinctive pattern, either bunodont or lophodont; divided into two suborders, the Duplicidentata (hares and rabbits) and the Simplicidentata (rats, mice, squirrels, and other rodents). The largest known rodent is a fossil,
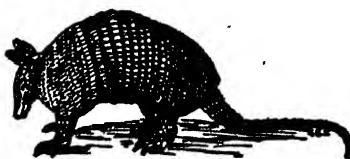
Armadillo   Sloth

FIG. 37

Castoroides, a beaver as large as a black bear, widely distributed in North America during the Pleistocene period. The largest rodent living today is the capybara of South America. Examples: (Fig. 38) Leporidae (hares and rabbits), Ochotonidae (conies), Muridae

(rats and mice), Sciuridae (squirrels), Castoridae (beaver), Erethizontidae (porcupines), Geomyidae (gophers), etc.

Order *Carnivora.* Unguiculate, flesh-eating mammals with small incisors and large canines; anterior molars
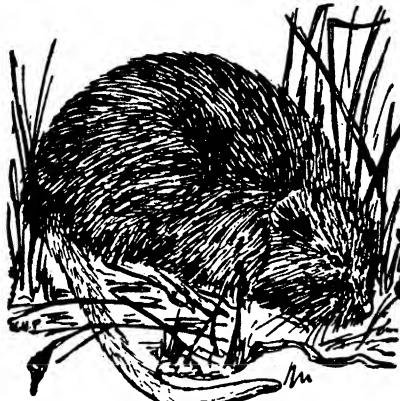
Fig. 38. Muskrat.

or premolars usually modified for shearing; clavicle rudimentary or lacking; divided into two suborders: the Fissipedia, living on land, comprise the Viverridae (genets), Felidae (cats), Hyaenidae (hyenas), Canidae (dogs and wolves), Mustelidae (weasels), Procyonidae
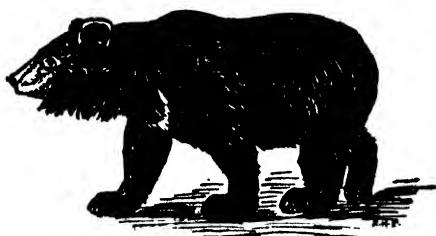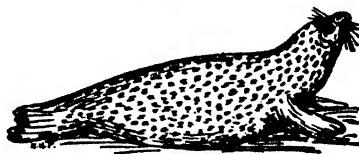
Bear   Seal

Fig. 39

(raccoons), Ursidae (bears); the Pinnipedia, living in water, with limbs modified to form paddles or flippers, comprise the Phocidae (seals), Otariidae (sea-lions), and Odobenidae (walrus). (Fig. 39.)

Order *Cetacea.* Sea-mammals with cylindrical bodies and smooth glandless skins; tail fin horizontal; nasal

openings far back on the skull roof; teeth peg-like if present; anterior limbs flipper-like with skeletal parts much modified; posterior limbs missing, with a few pelvic parts persisting as rudiments; adipose azygous fins. Examples: (Fig. 40) Balaenopteridae (whales), Delphinidae (dolphins), and Platanistidae (porpoises).
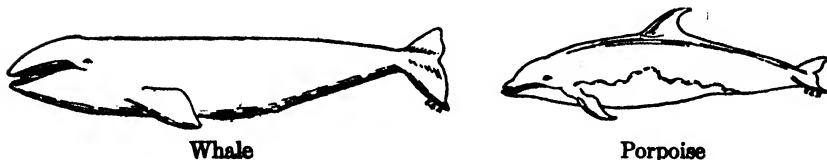
Whale   Porpoise

Fig. 40

Order . *Hyracoidea.* A small group of plantigrade-herbivorous-ungulates with hoofs; premolars and molars lophodont, four toes on anterior limbs and three on the posterior limbs. Example: (Fig. 41). Hyracidae (cony) of Asia.

Fig. 41.   Hyrax.

Order *Proboscidia.* Five-toed, herbivorous mammals with upper lip converted into a trunk; second incisors modified into tusks; molars lophodont or bunodont; canines missing; limbs straight. Examples: Elephantidae (elephants) (mastodons and mammoths in the past).

Order *Sirenia.* Herbivorous ungulates living in the sea, with anterior limbs paddle-like and posterior limbs missing; pelvic bones vestigial; teeth lophodont. (Fig. 42) sea-cows, dugong . (Halicoridae), manatee (Manatidae).
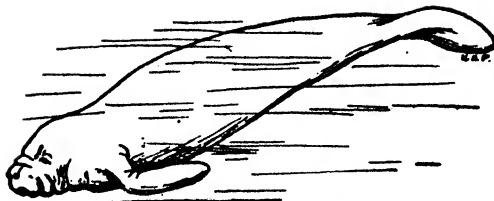
FIG. 42. Manatee.

Order *Artiodactyla*. Herbivorous ungulates, living mostly on land, with the axis of the foot between toes 3 and 4; toes 2–4 in modern forms; incisors and canines of upper jaw often missing; teeth bunodont, buno-selenodont, or selenodont; stomach sometimes complex. Examples: (Fig. 43) Bovidae (cattle), Cervidae (deer, musk deer, sheep), Suidae (pig), Hippopotamidae (hippopotamus), Giraffidae (giraffe), and, Camelidae (camel).
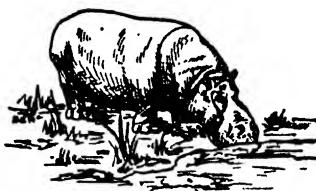
Antelope   Hippopotamus

FIG. 43

Order *Perissodactyla*. Herbivorous, land-living ungulates with axis of foot through toe 3; toes odd in number; incisors $\frac{3}{3}$; molars lophodont or selenodont; no gall bladder. Examples (Fig. 44) Equidae (horses, asses, zebra), Tapiridae (tapir), and Rhinocerotidae (rhinoceros). (Fig. 45.)

Order *Tubulidentata*. Plantigrade anteaters of Africa; claws greatly elongated; teeth enamelless and rootless. Example: (Fig. 46) Orycteropodidae (aardvark or *Orycteropus*).

Order *Primates*. Plantigrade, omnivorous mammals; usually with nails; orbits surrounded 'by a bony ring; pollux and hallux opposable; brain case usually large; molars quadritubercular or quintitubercular; incisors $\frac{2}{2}$.
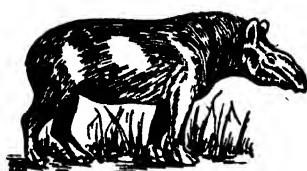
FIG. 44. Tapir.
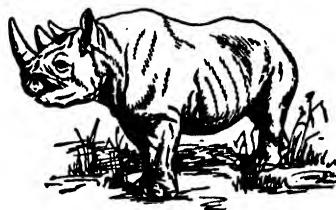
FIG. 45. Rhinoceros.
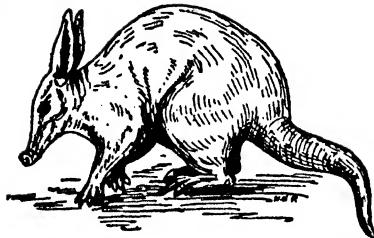
FIG. 46. Orycteropus.

FIG. 47. Lemur.
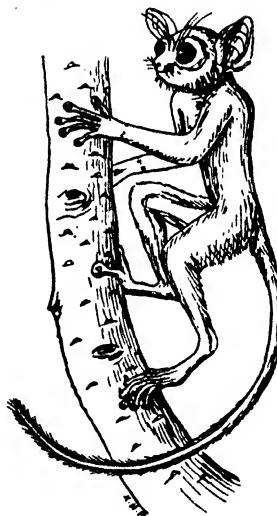
FIG. 48. Tarsius.

Suborder Lemuroidea. Low primates in which the brain case is small and the brain simple; nose elongate; arboreal; many nocturnal; inner incisors of upper jaw usually separated. Example: (Fig. 47) Lemuridae (lemurs), etc.

Suborder Tarsioidea. Small group of one genus; with a dentition of $\frac{2-1-3-3}{1-1-3-3}$; orbit separated by a bony partition from the temporal fossa. Example: (Fig. 48) Tarsiidae (tarsius).

Suborder Anthropoidea. Brain much convoluted and the cerebral lobes cover much of the cerebellum; mammae always pectoral; inner pair of incisors of upper jaw in contact. Examples: Hapalidae (marmosets), Cebidae (howling monkeys), Cercopithecidae (baboons, and monkeys of the catarrhine group), Hylobatidae (gibbons), and Anthropoidea (orang, chimpanzee, gorilla, man).

Early in 1939, a fish belonging to a group long thought extinct was dredged up from forty fathoms off the coast of East Africa. The new fish, named *Latimeria chalumnae* (Smith), belongs to the family Coelacanthidae, a subdivision of the crossopterygians. This discovery is of great interest to students of fishes, for finding a living specimen of a fish supposed to have been extinct for fifty million years is a real event in fish history. The group Coelacanthidae was supposed to have died out in the Cretaceous.

PART TWO

CHAPTER III

INTEGUMENT

The integument has several important functions: the formation of a pliable covering for the body, resistant to the entrance of foreign materials; the regulation of body temperature; the prevention of the evaporation of the body fluids; the excretion of waste through the sweat glands; the development of sense organs; and the formation of special coverings and appendages. The prevention of evaporation is not important in animals living in water, but it becomes vital in land animals, which require a thicker skin with an exterior layer of cornified cells.
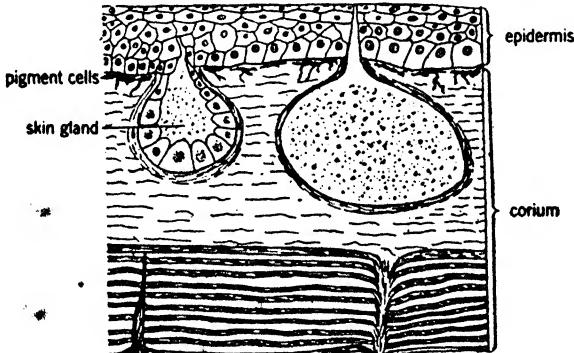
Fig. 49. Section of frog skin. After Schimkewitsch.

The skin consists of two layers: the outer layer, or epidermis, being of ectodermal origin; and the inner layer, or corium, being derived from the mesoderm (Fig. 52). The epidermis is usually thin, and from it are formed a number of structures, such as epidermal scales, feathers, hair, horns, nails, claws, and the enamel of the teeth. The epidermis may contain sensory cells, light organs (photophores), and poison glands. The epidermis may be divided into two sublayers, an outer layer of dead cells, which are usually flattened in land forms, and an inner layer of cubical cells, called the Malpighian layer, which is in contact with the nourishing materials of the corium. Blisters are formed by the separation of the Malpighian from the outer layer. The surface of the epidermis has openings for the glands that produce sweat, oil, and mucus.

The corium (Fig. 52), or dermis, is quite different from the epidermis, having a number of structures that are distinctive. This layer is usually thicker, and in its early embryological history it is derived from the outer layer of the myotome. The corium forms the leather of commerce. The main material of the corium consists of fibrous, connective, and elastic tissues, which give it strength. The corium is supplied with a rich series of blood vessels, with a network of capillaries and lymphatics extending over the whole surface of the body. Smooth muscles for the movement of the skin and its appendages are present. The sensory system consists of numerous types of sense cells, which are strictly specific in function, and some bare nerve endings in the form of a network. These sense cells may be quite close to the surface because of the folding of the epidermis. Sense cells are very plentiful on the finger tips and other restricted areas of the body. Most pigment cells are located in the corium, although a few may be found in the epidermis. Bone is commonly developed in this layer, primarily in the formation of scales of the bony type such as those of the sturgeon or garpike. Secondarily, this same type of bone formation is utilized in skeleton building, and the dermal bones come to be an important part of the skeletal system. All the dermal bones of the skull are considered to be modifications of scales or numbers of scales growing together in clusters to form bony elements. These dermal bones have Haversian canals and the structure of cartilage bone, so that in adult animals there is no means of distinguishing materials of these two different origins. The teeth consist principally of dentine, a material from the corium, but the outer enamel layer is a contribution from the epidermis. All the special epidermal structures, such as scales, teeth; feathers, hair, claws, nails, and glands, dip down into the corium and retain a connection by which they obtain nourishment. Some of these structures are shed periodically; others retain a permanent connection with the corium.

Skin of the Different Classes of Vertebrates

The skin of *Amphioxus* consists of but one layer of epidermal cells, and in this it resembles the invertebrates. The placoderms, much lower than the fishes in organization, had species with a covering of small denticles, as well as many species with well-organized systems of protecting plates.

Skin of Fishes. — The skin of fishes (Fig. 50) is rich in mucous glands, which supply a protective coating, prevent the entrance of foreign materials and the growth of fungi, and make the skin smooth so as to reduce the friction in passing through the water. Poison- and light-producing

organs may be present. In some fishes the scales develop from the corium alone; in others they develop from both layers of the skin. The scales, though subject to many variations, are of four general types: placoid, ganoid, cycloid, and ctenoid.

Placoid Scale. — The placoid scale (Fig. 51 *A*) of the shark is important since it is assumed to be the origin of teeth, and probably also of other structures of higher vertebrates. Primitively the placoid scale consists of a flat base, buried deep in the corium, from which a cusp projects to the outside of the skin. In origin the scale is from two sources, the dentine from the corium, and the enamel from the epidermis. Each scale has a permanent cavity, large in the developing scale but reduced in the adult structure, filled with a pulp by which blood vessels, nerves, and other structures retain their connections The shark tooth appears to be a placoid scale drawn into the mouth, with all the scale characteristics. In many sharks there is a perfect intergrading of the scales into teeth.
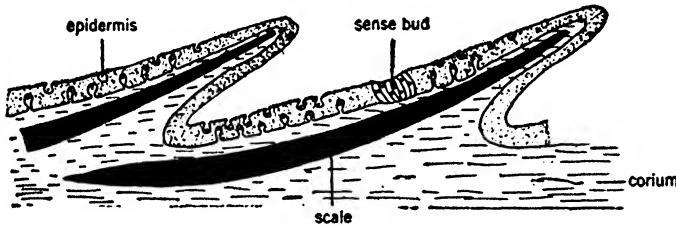
FIG. 50. Section of skin of teleost. After Maurer.

Ganoid Scale. — The ganoid scale is a collective name applied to a number of structures from quite different and unrelated fishes. These are heavy and quite complex in their structure, having a shiny coating of ganoin that is not epidermal in origin in spite of the resemblance. The scales of this type (Fig. 51 *C*) are generally rhombic in shape and do not overlap, but are joined by small peg-and-socket mechanisms which permit some movement. Once a very common covering of fishes, this type of scale is now restricted to a small number of species. The scutes, or plates, of the sturgeon represent a number of joined scales.

Cycloid Scale. — The cycloid scale found in *Amia* (Fig. 51 *D*), *Neoceratodus*, trout, and other lower groups of fishes, is rounded in outline and is strictly a product of the corium.

Ctenoid Scale. — The ctenoid scale (Fig. 51 *B*) differs from the cycloid in that the free edge is lined with prickles or spines, which may be soft, or harsh and rough   This type of scale is found in the higher fishes.

Dermal Bone of the Fishes. — The origin of the dermal bones may be seen in all stages in the lower fishes, where dermal plates are added to the chondrocranium and to other parts of the skeleton, and thus function in the building of bones. Such bones retain their characters as plating bones, with sculpturing and lateral-line canals, while those in the mouth cavity carry in with them the scales modified as teeth.
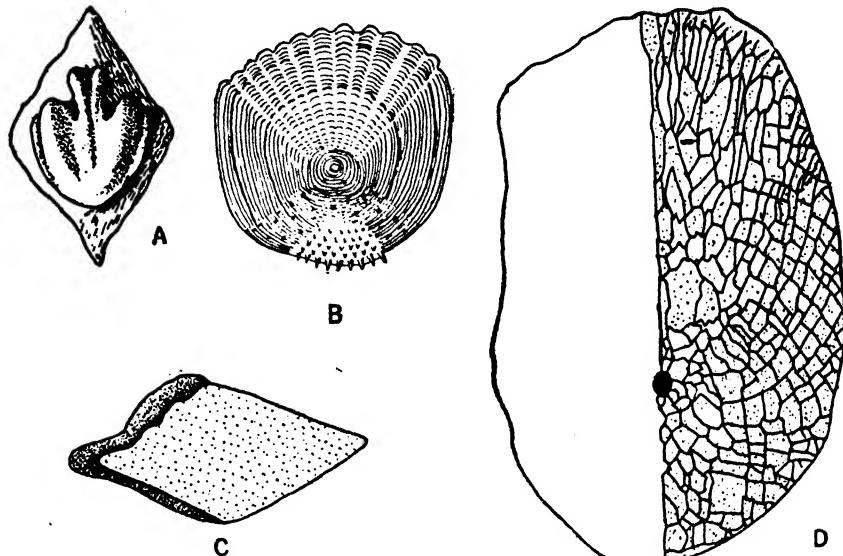
FIG. 51. Types of fish scales. A, placoid (shark); B, ctenoid (bluegill); C, ganoid (gar); D, cycloid (lung-fish).

Skin of Amphibians. — The skin of the amphibians (Fig. 49) is thin, with large lymph spaces separating it from the muscle layer underneath. In the water-living forms the skin is richly supplied with mucous glands; in land forms it is less glandular. No scales are present in modern amphibians, except in the Gymnophiona which have them imbedded in the skin, although the fossil stegocephalians were well covered with typical scales. Chromatophores are usually present, and some members of this class have the ability to make decided changes in color. The skin of the amphibians is generally quite porous, since it serves a most important function as an accessory respiratory organ, but toads and land-living forms have a slightly hardened epidermis which prevents too much loss of moisture. Claws are generally lacking among amphibians.

Skin of Reptiles. — With reptiles the first land skin is developed in which there is a perfect protection against a loss of body fluids. In contrast to the fishes and amphibians, reptiles have a layer of dead cells in contact with the air. The skin of reptiles may be entirely impervious

to water although, in some desert forms, practically the whole supply for the uses of the body must be soaked in through the skin. They usually are covered with either epidermal scales or bony plates. The epidermal scale is formed by the folding of the epidermis on the dermis; in the development of the bony plate a papilla is formed, similar to that in the development of the placoid scale of the shark. Lizards and snakes shed their epidermal covering periodically. Some of the extinct reptiles, particularly the water-living ichthyosaurs and the flying pterosaurs, had a smooth skin without scales. Others were covered with bony plates of dermal origin, such as are now found on the Crocodilia and Heloderma (Gila monster). Most modern turtles retain both the bony
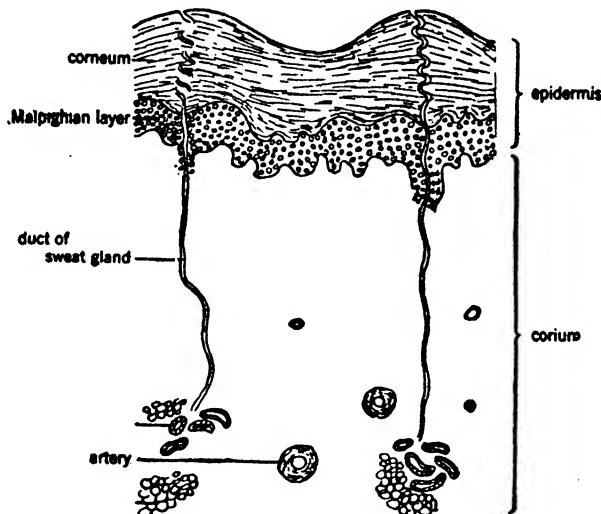
FIG. 52. Section of mammalian skin.

plates and the epidermal scales, and all of them have epidermal sheaths on the jaws. The soft-shelled turtles (Trionychia) and the leatherback sea-turtles (*Dermochelys*) have lost the epidermal scales and most of the bony plates, leaving a leathery covering — a return to water conditions. The skin glands of reptiles are usually localized around the mouth, on the thigh (femoral glands), and near the anus. In some of the lacertilians the rapid changing of color is an automatic response of the chromatophores, or pigment cells, to surrounding conditions. Reptiles may develop accessory structures such as spurs, spines, and horns. Claws are practically universal within the class.

Skin of Birds. — The skin of birds (Fig. 53) is thin and without glands except in a restricted area at the base of the tail, where the

uropygial gland produces an oil that is used for dressing the feathers. The typical covering of birds is the feather, which is considered a modified scale. Feathers are not distributed uniformly over the entire body, but are confined to areas called pterylae, in contrast to the apteria, or areas without feathers. Feathers are shed at intervals, usually in the summer so that the plumage is complete at times of migration and during the cold seasons. The feather (Fig. 55) is admirably adapted to the needs of birds, since it is light, warm, and strong, and hence serves both as a flight structure and as an insulator. Feathers are divided into several types, each with its special uses: (1) pennae, the typical contour feathers; (2) remiges, or flight feathers; (3) plumulae, or down feathers; and (4) filiplumes, or hair feathers. Coloring, so striking in birds, is due primarily to pigments in the feathers and secondarily to their prismatic surfaces which give rise to the iridescence.
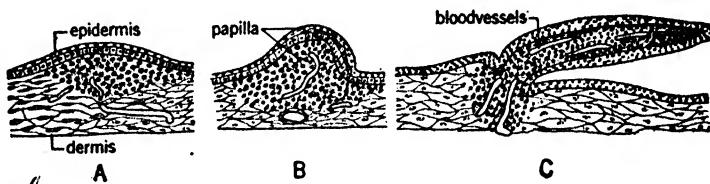
FIG. 53. Developing feather. A, early stage of papilla; B, papilla enlarged; C, early stage of feather.

The development of the feather (Figs. 53, 54) is similar to that of the scale, the origin being a papilla formed from the dermis, with an epidermal covering. This sinks in slightly and comes to lie in a feather follicle, from which the growing feather protrudes. The completed feather is purely ectodermal. Although the feather is considered a modified scale, the process of its transformation is entirely unknown and remains a problem. The first known bird, *Archaeopteryx*, had fully developed feathers. In modern penguins the feathers of the wing revert to scale-like structures once more.

Birds have but few epidermal structures aside from the feathers. Spurs are quite common on the legs and occur in a few cases on the wings, where they represent vestigial claws. The bill has a horny epidermal sheath, and the legs retain reptilian scales. It is probable that the horny sheath of the bill was not present in early forms, such as *Archaeopteryx*, which had teeth.

Skin of Mammals. — The skin of the mammals is of the typical land type with a cornified layer of dead cells forming the outer layer, or corneum (Fig. 52). Under this is the growing Malpighian layer, which is in contact with the corium. No living cells are exposed to the air

except those around the orifices. The greatest specialization of the two layers is reached in the mammals, with their high differentiation and general adaptability. The most striking difference between the skin of mammals and that of all other vertebrates is the presence of sudoriparous, sebaceous, and mammary glands. In general the mammalian skin, with its higher development of the corium, is thicker than that of the lower forms. The covering is hairs, instead of scales or feathers.

The development of the individual hair parallels that of the feather and scale. It starts by a thickening of the epidermis which dips down into the corium, and from this pit a solid horny shaft is pushed outward by the rapid growth of these specialized epidermal cells, which get their nourishment from the corium. This connection remains, and when the hair is shed the break is well above this root, or matrix, so that regeneration follows easily. The hair itself becomes organized and divided into regions, a central medulla, a middle cortex, and an outer cuticle. Small muscles in the corium are able to change the position of the hairs, thus causing the gooseflesh evident when the human body is exposed to sudden cold. Before birth an embryonic coat of hair, the lanugo, is quite evident, but it is shed soon after birth. The hair pattern (Fig. 56) is quite regular and seems to suggest that the first hairs developed around scales, a condition still to be found in the armadillo.

FIG. 54. Developing feather in follicle.

There are many modifications of hair in the mammals, due to differences in both structure and shape, an extreme being reached in the porcupines with their special quills. Horns of the type found in the rhinoceros and antelope appear to be formed by bundles of hair massed together. The shape of the hair may be cylindrical or flattened and roughened on the outside. The soft wool of animals such as the sheep or beaver is hair with a tendency to curl, because of the flattened shape and rough exterior, which aids in felting. The eyes are usually protected by elongated hairs, the eyelashes; and whiskers, or vibrissae, which have a well-developed nerve supply at their bases, may grow around the mouth. The hair is arranged in stream lines pointing in different directions. In man there is usually a whorl in the occipital region; in other mammals there may be a number of these whorls in

different regions of the body. The hair carries pigments, giving black, brown, or reddish colors. Melanistic and albinistic mammals are not uncommon.

Scales appear commonly in the mammals and seem to be a part of their heritage from the reptiles. Embryos may show scales or spines that are not at all evident when they are born. The embryo of the bear has a complete development of spines in the skin, which are entirely lost with further growth. Scales appear on the tails of many mammals, including the rats, mice, muskrats, and beaver, but these scales are not
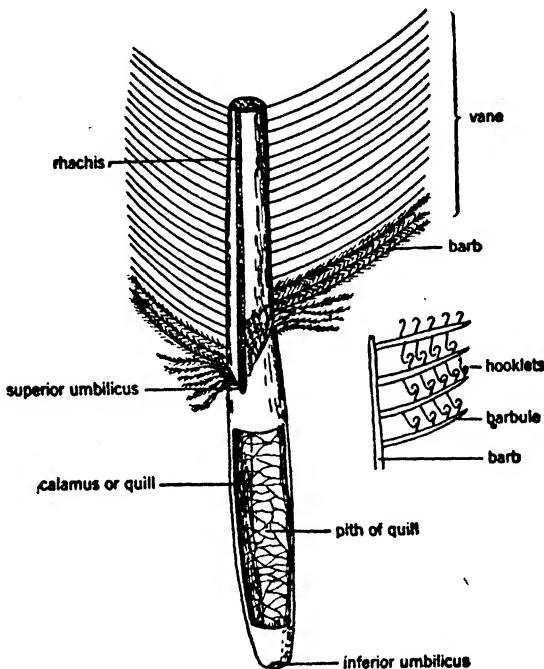
FIG. 55. Parts of a feather.

overlapping, and hairs are interspersed between them. The feet of kangaroos are strikingly scaled, even in the adult stage, and the palms and soles of other mammals, including man, show many evidences of a scale pattern. The most perfect mammalian scales are found in the pangolins; they are purely epidermal scales, often two inches in length, which overlap and have the typical reptilian arrangement. Bony plates are found principally in the edentates; the armadillo, a modern representative of this once large group, is completely covered with bony plates, with hairs arranged around the edges.

Claws and nails, purely epidermal structures, have become very

highly specialized in the mammals (Fig. 57). The claws fit over the ends of the last bones of the digits and are modified cones in appearance. Without specialization, the claws (Fig. 57 C) protect the ends of the digits and may give some traction in walking. By broadening and strengthening, they are fitted for digging, as in badger or mole. Those used for climbing are thin and sharply pointed, and by their aid semi-arboreal mammals are able to live in trees. The cats have developed sharp, curved claws that are very useful in holding and killing their prey. The hoof (Fig. 57 D), found principally in the "ungulates," is a modified claw that forms the contact with the ground. In the horse the hoof is developed from the claw of only one toe, with no other parts of the foot touching the ground. Other hoofed animals may use
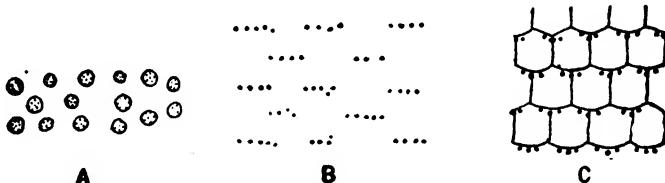
FIG. 56. Grouping of hairs in mammals. A, beaver; B, monkey; C, rodent. After Meijere.
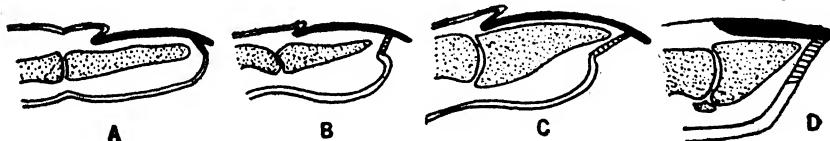
FIG. 57. Sections of claws and nails. A, nail; B, claw; C, claw; D, hoof. Redrawn from Boas.

other parts of the foot, or may be provided with spongy pads, such as are found in mountain sheep, where a hard hoof would not serve well for rock climbing. The nail (Fig. 57 A, B) perhaps the highest development, is found in the higher primates and in a few species of other orders. It is a flat structure that does not form a cap over the end of the digit, but merely a dorsal plate.

Horns are conical, epidermal caps that develop on solid cores arising from the frontal and parietal bones. The median horn of the rhinoceros appears to be formed from firmly appressed hairs, and it is quite possible that other horns have the same organization. Horns grow continuously, and are not shed except in the antelope (*Antilocapra americana*), which sheds a part of its horn and which also is the only mammal with a branched horn. If lost, horns are not replaced, since no regeneration takes place. Generally but one pair is present, but some of

the domestic breeds of sheep (Navajo sheep) have two well-developed pairs. Some of the early mammals (titanotheres) had several pairs of horns. In modern mammals, horns and antlers are practically confined to the Artiodactyla.

Antlers are entirely different from horns, since they are formed from bone and are usually branched. They start their growth as small protuberances on the skull bones, usually the parietals, and remain covered by a layer of epidermis until they have attained their full size and growth. This epidermal skin is called the velvet and is coated with hair. After growth is completed, the covering loses its vascular connections, dies, and is rubbed off, leaving the antlers in their prime. Some of the antlers of the deer group are enormous, those of the extinct Irish elk having a spread of thirteen feet. Antlers are shed annually by means of the formation of a constriction below the burr, so that they
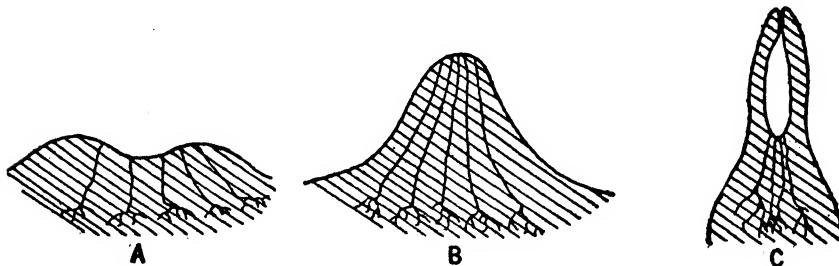
FIG. 58. Schema of developing nipples. A, primitive condition as in monotremes; B, marsupial; C, placental mammal. After Weber.

are easily dropped off in the winter or early spring, an immediate new growth starting for the next pair.

Glands. — In contrast to the almost glandless skin of the reptiles and birds, that of the mammals is richly supplied with several types of glands. (Skin glands are lacking in whales and sea-cows.) Both the sweat (sudoriparous) glands and the oil (sebaceous) glands appear to have their origin in connection with the growth of the hair, and whereas the oil glands usually retain this association, the sweat glands are generally spread over the skin. The oil glands are acinose in form (like a bunch of grapes) and have their outlets along the side of the hair. In the region of the eyes the Meibomian glands become separated from hair.

The sudoriparous glands are tubular in form, opening through the epidermis by means of pores. They extend through this layer of the skin by a coiled tube, and the body of the gland itself is deeply imbedded in the corium, where it is in contact with the capillaries. Perspiration is a means of elimination of salts and other waste matters, besides being an aid in the stabilization of temperature. The character of the se-

cretion varies, since in man it is watery and colorless, in the horse it is mucilaginous, and in the hippopotamus it has a distinct red color.

Scent glands, which probably have a function connected with sex, are modified sebaceous glands, and hence are of the acinose type. These include the anal glands of the skunks and other Mustelidae, suborbital glands of the deer, preputial glands of the beaver and musk deer, temporal glands of the elephant, and numerous other glands found in other orders.

Most striking of all are the mammary glands (Fig. 58), by which the mammals are distinguished as a separate class of the highest vertebrates. These milk-producing glands are tubular, and this is one reason for assuming that they originated from modified sweat glands. They probably became specialized in connection with certain brooding areas or ridges on the ventral sides of the females, similar to the ridges that develop in birds while incubating eggs. Originally the fluid from these glands poured out over the surface, as in the monotremes, with no nipples. The system is more specialized in the marsupials, where nipples are present, and it reaches its highest development in the placental mammals, where the glands are closely associated with the bearing of the young and function during their infancy, drying up later when no longer needed. This milk-producing function is intimately associated with the longer period of infancy.

Dermal Bone. — The development of dermal bones, or membrane bone, from the corium of the skin, has been of great importance in supplementing the skeleton, especially in the head and shoulder region. The dermal plates of the skull have been added to the chondrocranium and supply a complete covering except in the occipital region. The jaws, or mandibles, originally made entirely of cartilage, have been surrounded with membrane bone, so that in the higher vertebrates Meckel's cartilage becomes but a vestige. Bones of dermal origin added to the shoulder girdle include the cleithra of fishes and amphibians and probably parts of the clavicles. Parts of the sternum in certain of the reptiles have been added from the dermal layer, and the gastralia, or belly ribs, of the Crocodilia, *Sphenodon*, and *Archaeopteryx* are formed from this material.

Teeth

The origin of teeth appears to have been from placoid scales, and a comparison of the development of both is quite convincing, since the processes are practically identical, each starting in the same way and carrying through to a mature structure in a similar manner (Fig. 59).

The presence of teeth in the mouth can be explained by the fact that, in the developing embryo, the oral cavity comes to be lined by a layer of ectoderm that is drawn in from the surface, carrying with it its tendency to develop epidermal appendages. In some of the elasmobranchs it is possible to trace a graduated series of scales into the mouth cavity, with no break in the continuity. Even in the higher vertebrates, such as the mammals, this tooth formation follows the same general plan, and there can be no question of the origin. Whereas the teeth of all the lower vertebrates are comparatively simple cone-like structures, the teeth of mammals become highly specialized, with additional cusps and often with very intricate patterns on the grinding surface.
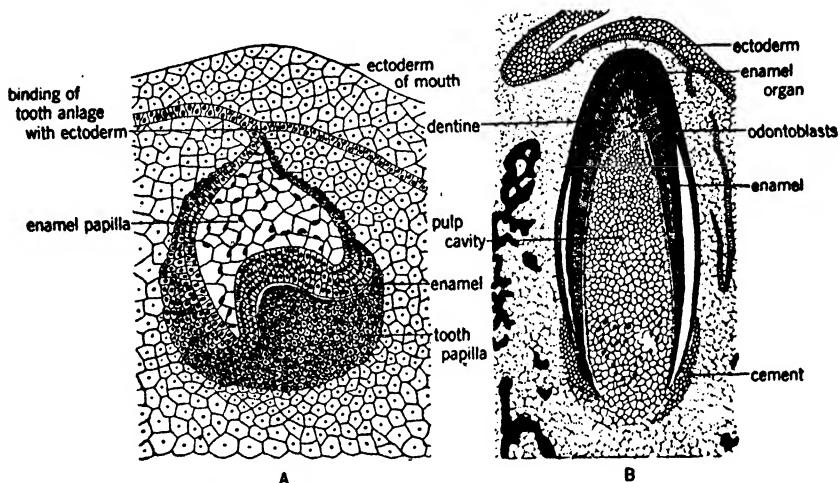
Fig. 59. Developing teeth of pig, slightly diagrammatic. A, developing molar showing the relation of the growing parts and the formation of the tooth; B, developing canine tooth.

The rasping teeth of the cyclostomes are of purely epidermal origin and contain no dentine. The epidermal teeth that develop as temporary structures in young amphibians are lost later or replaced with real teeth. Epidermal plates, not comparable to teeth at all, appear in turtles and modern birds, where they serve to protect the jaws. The monotremes have real teeth in their developmental stages, but these are lost and replaced by epidermal plates in the adult forms (duckbill).

The attachment of teeth to the jaws is quite variable in the vertebrates. In fishes, amphibians, and some reptiles, the teeth are lost and replaced constantly, but in a few reptiles and in mammals there is a more limited growth of new teeth, only one or two sets being developed. Those of the sharks are fixed to the jaws by fascia and tough

connective tissue. The manner of attachment to the jaws is called acrodont (Fig. 60 *A*), if the tooth is placed upon the crown of the jaw, pleurodont (Fig. 60 *B*) if it is ankylosed to the inside of the jaw, and thecodont (Fig. 60 *C*) if it is in a pit on the crown of the jaw.· With the development of the higher types of teeth and relative permanence, roots are formed, and there is a specialization of the pulp cavity for nourishment.

Teeth of Fishes. — Teeth may appear on almost any bone of the oral cavity of fishes. There is a striking development of teeth in the sharks (Fig. 61 *A*, *B*) most of them having a general similarity in shape not
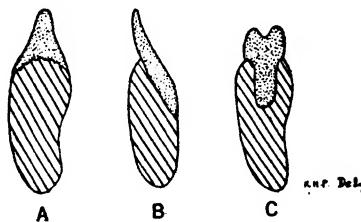
Fɪɢ. 60. Different types of tooth attachment. A, acrodont; B, pleurodont; C, thecodont.
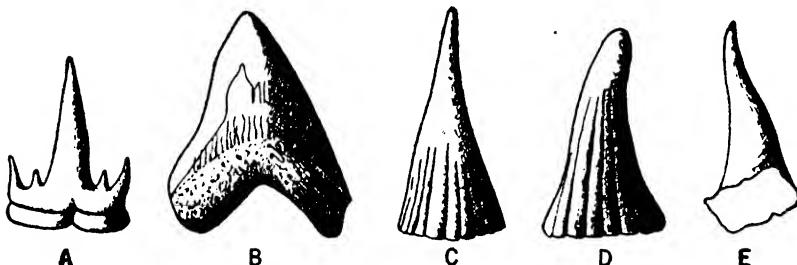
Fɪɢ. 61. Teeth of fishes. A, Cladodus (after Dean); B, Carcharodon, an Eocene shark; C, Lepisosteus; D, Anarrhichthys; E, Esox.

found in any of the other fishes. Some have several cusps, and many have serrated edges, but all are very effective cutting instruments. The peculiar " pavement " teeth of some of the rays mark them as eaters of molluscs; other carnivorous fishes, such as the pike, garpike, pickerel, and bowfin, have long, sharp, needle-like teeth (Fig. 61 *C*, *D*, *E*). Crushing teeth are found in some of the teleosts. Anarrhichthys has a very efficient series of heavy crushing teeth (Fig. 75), well adapted for the uses of this fish. The teeth are greatly reduced or absent in many of the teleosts, since their food requirements are such that teeth would be of no particular value. The spoonbill (*Polyodon*) and other fishes that live on plankton, obtained by straining water, are usually

toothless. The peculiar tooth-like structures appearing on the pharyngeal bones of the carp, though they are used as teeth and are covered with an enamel-like layer, have a different origin and are not homologous structures.

Teeth of Amphibians. — The teeth of modern amphibians are always small, needle-like, and inconspicuous and are but little differentiated. The fossil stegocephalians had large teeth, often with a very complicated enamel pattern, as in the labyrinthodonts. The attachment is usually to the side of the jaw and hence pleurodont. The distribution of the teeth is more restricted than in the fishes, since they generally are found only on the premaxillae, maxillae, palato-pterygoids, coronoid, dentary, and vomero-palatines, but not on other bones of the oral cavity.
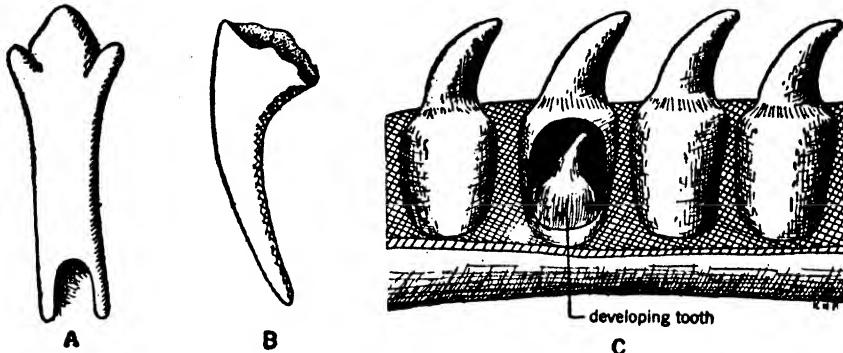
FIG. 62. Teeth of reptiles and birds. A, iguana; B, python; C (after Marsh), Hesperornis regalis, showing developing teeth.

Teeth of Reptiles. — Reptiles are generally provided with teeth. The turtles are the exception in having no teeth and in being provided with horny plates comparable to those of the bird bill. The teeth may be divided into two groups, those suited for animal food and those specialized for herbivorous diet. There is a constant loss and replacement of teeth, with little of the permanency found in the mammals. The attachment may be acrodont as in *Sphenodon*, or pleurodont as in the Iguana (Fig. 62 *A*), or thecodont as in the alligator. With the exception of the Therapsida, no order or group has any specialization of the teeth that would suggest the mammalian dentition. Inasmuch as most reptiles swallow their food whole, the most efficient tooth for them is one that is long and sharp enough to assist in holding the prey, and this is the type found in carnivorous forms. The extinct fish-eaters, such as the ichthyosaurs, had needle-like teeth, superficially resembling those of the fishes, such as the garpike, that get their food in a similar manner. The carnivorous dinosaurs (*Tyrannosaurus*) had teeth that

were dagger-shaped, with sharp edges, so that they were of value in killing as well as in holding. The teeth of the snakes (Fig. 62 *B*) are very long and sharp but rather weak. The poison fangs are developed for the special purpose of introducing the venom into the wound and are not essentially killing teeth. A tube for the passage of the poison is formed by a secondary fold of the wall of the tooth (Fig. 63 *A*, *B*, *C*).

The herbivorous reptiles have teeth with flattened crowns, which form a grinding surface. The teeth of *Trachodon* and other dinosaurs of this type were very efficient in handling masses of vegetable material. The most extreme crushing dentition is that found in the fossil *Placodus*, and the arrangement suggests that the animal lived around or in water and used the teeth for crushing molluscs and other shelled food.
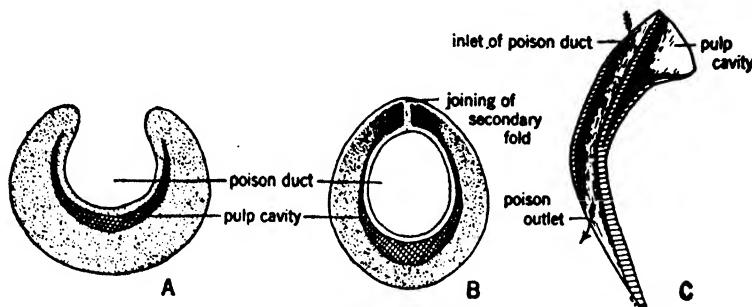
Fig. 63. Poison fangs. A, cross-section of grooved tooth of Heloderma; B, cross-section of fang of a rattlesnake; C, sagittal section of poison fang of rattlesnake.

Teeth of Birds. — Only the earliest birds had teeth. In *Archaeopteryx* of the Jurassic period and in *Hesperornis*, *Ichthyornis*, and other birds of the Cretaceous period, the teeth were typically reptilian and were probably useful in food-getting. *Hesperornis*, a diver, living in the Cretaceous sea of Kansas, certainly could make good use of the sharp-pointed teeth (Fig. 62 *C*). Teeth do not appear in any birds of the Tertiary or Quaternary periods, although they can be demonstrated in the developing young of some modern forms. Ducks have an adaptation of the horny covering of the jaws that forms a strainer, and in the fish-eating ducks the serrated edge of the mandible serves for holding the prey.

Teeth of Mammals. — The mammalian dentition becomes highly specialized with a number of features not found in the reptiles. Instead of a constant replacement, the number of sets of teeth is limited. Usually the first, or milk set is shed and is followed by a permanent set that must last throughout the life of the animal. The differentiation initiated by the therapsid reptiles is continued, with standardization of

the teeth into four kinds: incisors, canines, premolars, and molars (Figs. 64, 65). With few exceptions, the teeth are set in alveoli and held in the jaw by single or multiple roots. If the roots remain open, the growth of teeth may continue through the life of the animal; but if the roots close, so that only a small foramen remains for the nerve and blood vessels supplying the pulp cavity (Fig. 65 A, B), growth stops at a definite point. There is much diversification of the teeth them-
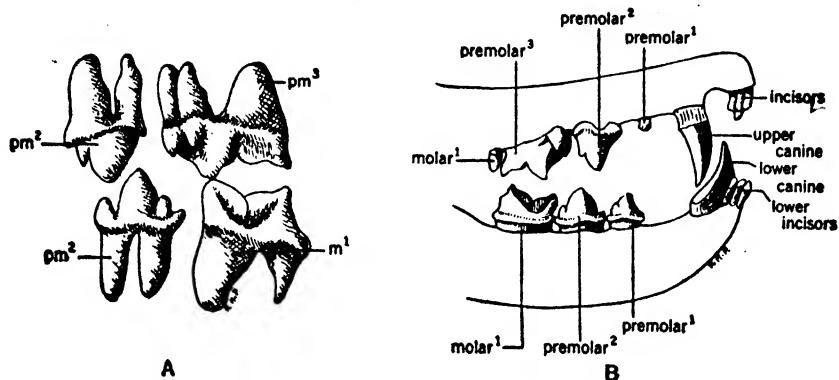
FIG. 64. Occlusion of teeth in cat. A, occlusion of the shearing teeth; B, occlusion of the entire dentition. After Jayne.

selves, with cusps of different types developed in connection with food specialization. The number also reaches a certain standardization with the following formula as fairly typical:

$$\frac{3\text{-}1\text{-}4\text{-}3}{3\text{-}1\text{-}4\text{-}3} = \frac{3 \text{ incisors}}{3 \text{ incisors}} + \frac{1 \text{ canine}}{1 \text{ canine}} + \frac{4 \text{ premolars}}{4 \text{ premolars}}$$

$$+ \frac{3 \text{ molars (in each half of the upper jaw)}}{3 \text{ molars (in each half of the lower jaw)}}$$

The division of the teeth into different types in the mammals has enabled them to specialize in ways not possible to the reptiles. The incisors (Fig. 64 B) are small in carnivorous animals, where they are used in a limited way, but in the herbivorous types they assume great importance, as in the rodents. The canines (Fig. 64 B) assume great importance in the carnivorous animals, serving for both killing and tearing; they are extremely large in many carnivores, but may be altogether absent in herbivores. The premolars and molars (Figs. 64 B, 65 B) have much the same use in the herbivores, but in the carnivores there is a tendency to develop certain of these into shearing teeth for meat-cutting (Fig. 64 A, B).

From a study of the dentition of the older mammals, Cope and Osborn developed a theory (Fig. 67) that the primitive type of the mammalian tooth was tritubercular, that is, with the three cusps in a triangle. According to this theory, the single spike-like *haplodont* (Fig. 66 *A*)
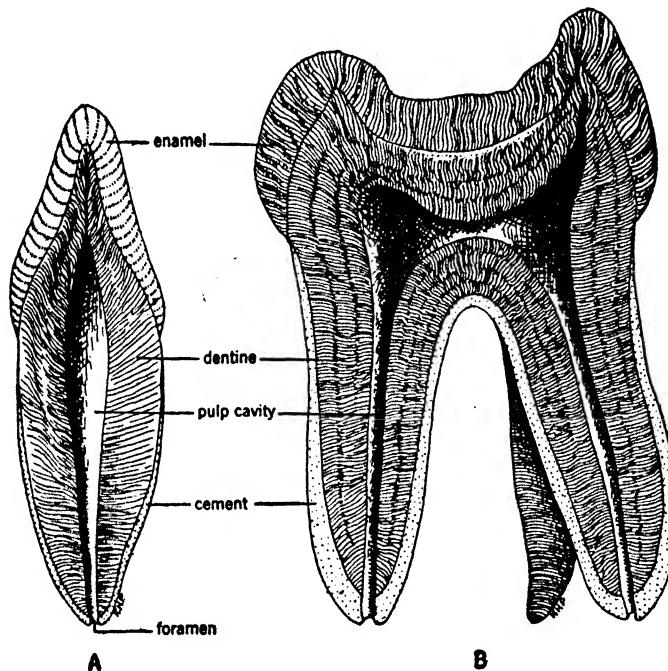
FIG. 65.   Section of teeth to show structure.   A, incisor; B, molar.   After Weber.
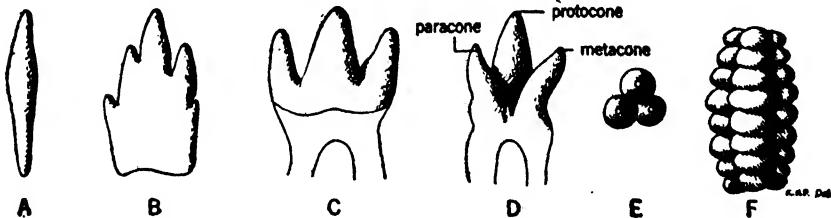
FIG. 66.   Development of tooth cones.   A, haplodont; B, protodont; C, tricono-
dont; D, tritubercular; E, triangular arrangement of cones in tritubercular;
F, multitubercular.   After de Terra.

tooth, now found in no mammals but the Cetaceans, is considered the original element from which the more complicated teeth have been derived.   The *protodont* tooth (Fig. 66 *B*), as found in the lowest fossil mammals, has small projections developing along the sides but with rather an indefinite organization of the cusps.   The *triconodont*
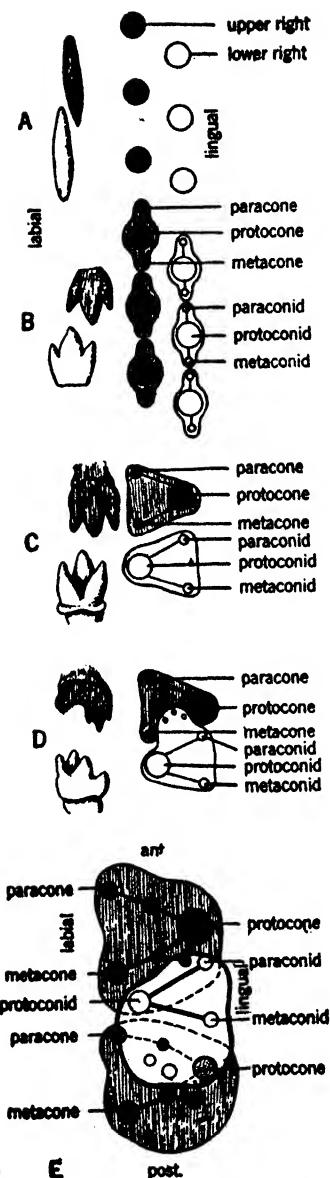
FIG. 67. The shifts and movements of the original cusps, as developed by the Cope-Osborn theory. After Osborn.

tooth (Fig. 66 *C*) has three definite cusps, all in a line, the central cusp usually larger and longer than the others. The turning of the smaller, lateral cusps produces the *tritubercular* tooth (Fig. 66 *D*) in which the cusps form a triangle, with the position reversed in the lower jaw, so that there is close occlusion. The number of cusps may increase to four or five or more, and one primitive group has a multitubercular pattern (Fig. 66 *F*).

The theories of Röse, Bolk, and others arrive at the same tritubercular tooth pattern, but in a different way, since they consider that the process of cusp-building was through the combination of small, single cusped teeth which would join together and thus form the tritubercular stage. The theory of Röse is called the concrescence theory and is based upon the formation of teeth combined from several single elements that appear in sharks, and from some considerations of conditions that occur in the development of the teeth of mammals themselves.

The discovery of a number of small Cretaceous mammals in Mongolia, and the restudy of the whole Mesozoic series of early mammals by G. G. Simpson, have shed much light on the evolution of the mammalian teeth, long a controversial subject among paleontologists. Although the main idea of the Cope-Osborn theory may be retained, certain details of the shifting of cusps in both the upper and lower molars must be restated, since some of their shifts of cusps and homologies of cusps have not been supported by paleontological evidence.

The height of the crown varies from the low-crowned (brachydont) type as found in the cow, to the high-crowned (hypselodont) type

as found in the horse. The tooth surface becomes highly specialized in the mammals, the carnivores developing a dentition (secodont) in which the teeth are specialized for meat-eating. This carnivorous dentition is found in a number of the orders, including the moles and
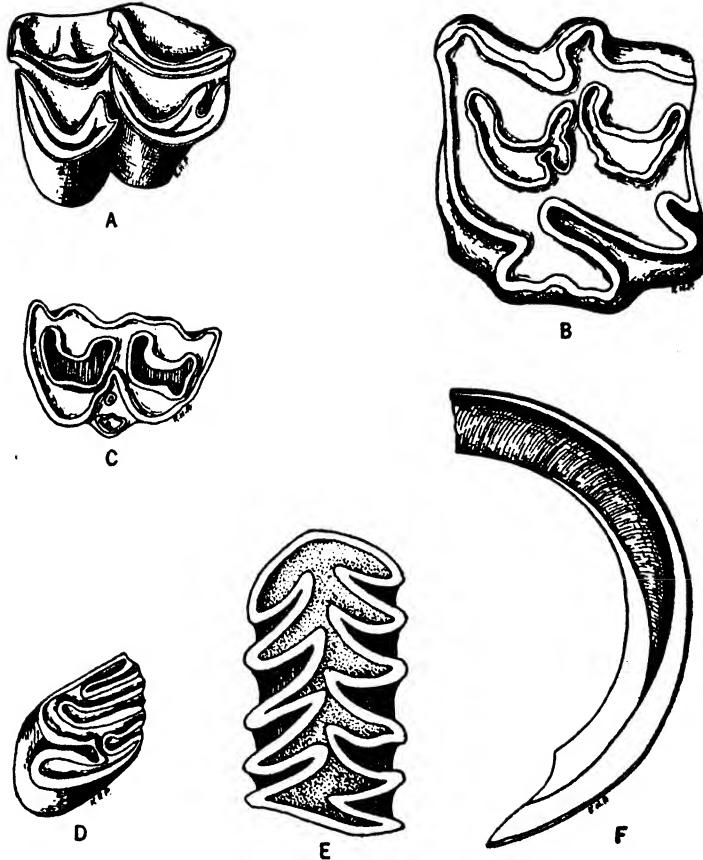
Fig. 68. Mammalian teeth. A, upper molar of moose; B, upper molar of horse; C, upper molar of cow; D, upper molar of beaver; E, first molar in lower jaw of muskrat; F, sagittal section of incisor of squirrel showing pulp cavity.

shrews (Insectivora), some marsupials (polyprotodonts), and the bats (Chiroptera). The carnivorous dentition varies from the most specialized type as found in the cats, to the modified, rounded, crushing cusps found in bears. The herbivorous animals including the hoofed groups such as the artiodactyls and perissodactyls have a dentition (selenodont) (Fig. 68 A) in which the enamel is folded with cement introduced between the folds, so that with the unequal wear, hard enamel ridges remain, thus forming sharp grinding surfaces (Fig. 68 E). This is

modified in the horse (Fig. 68 *B*) by the formation of cross ridges and crests (lophodont) (Fig. 68 *C*), and although the dentition is useful in grinding, it is not able to crush and cut vegetable fibers as does the selenodont type. The teeth of pigs are modified by the formation of rounded cusps (bunodont) which supply them with a dentition suitable for their omnivorous habits. Sometimes the types are mixed, as in the ancient titanotheres, in which the selenodont was combined with the bunodont, half of the tooth with cutting edges and the other half with rounded cusps. Since the type of dentition is closely correlated with the food habits, it is quite possible to determine these from a study of the dentition alone.

Résumé

The integument of vertebrates is important because of its many functions: it regulates the temperature of the body, controls the rate of evaporation of moisture, prevents entrance of foreign materials, aids in excretion of waste, and produces protective coverings (scales, feathers, hair, etc.), appendages (horns, tusks, etc.), and teeth. The skin consists of two layers: the outer layer, or epidermis, which is of ectodermal origin, produces hair, scales, feathers, horns, nails, claws, enamel of teeth, and glands of several kinds; and the inner layer, or corium, of mesodermic origin, which produces bone and dentine, contains blood vessels, nerves, and lymph vessels, and supplies nourishment for the epidermal structures. The skin of fishes is rich in mucous glands and usually is protected by scales or bony plates. The amphibian skin is thin and has numerous mucous pores and lymph spaces. The skin of reptiles is suited for life on land, being dry and tough, as a rule, and it usually is covered with scales or plates. The feathers of birds and the hair of mammals appear to be related to scales in their origin. Horns are formed by a thick growth of epidermis over a bony core; antlers are of mesodermic origin. The teeth of the lower vertebrates, originating from placoid scales, are usually peg-like and are frequently replaced; those of the mammals are differentiated into four types (incisors, canines, premolars, and molars) and are replaced but once or not at all. The mammalian molar is derived from the reptilian tooth through a specialization of the cusps. The Cope-Osborn and Röse theories explain the origin of tritubercular teeth. The discovery of new Cretaceous mammals in Mongolia, the restudy of the Mesozoic mammals by G. G. Simpson, and recent work by Gregory and Simpson, on the whole problem of trituberculy, have done much to clarify some of the obscure points in the tooth evolution of the mammals.

CHAPTER IV

SKELETAL ·SYSTEM

The skeleton is one of the most interesting parts of the vertebrate body, since it is intimately associated with every activity of the animal. This framework can be understood only in the light of a knowledge of the long series of changes through which the vertebrate animals developed — changes which have left indelible impressions on the bones, either in the embryo or in the adult. The musculature has been most closely associated with the development of the skeleton, but the nervous and vascular systems also have had their effects and left their marks on the bones. The skeleton is about all that remains of the animals of past ages, but fortunately it contributes greatly to our knowledge of the fossil forms because of its many indications of the softer materials that have not been preserved.

The chief source of bone is the mesoderm. The greater part of the skeleton is first formed in cartilage and is later transformed by a series of changes through which it becomes real osseous material with a characteristic structure. A second type, the membrane bone, is formed in a different way and goes through no cartilaginous stage. Originally the membrane bone is on the outside of the body and developed from the corium. In higher forms these two types of bone are closely joined, and their origin can be determined only by a study of their embryonic development.

For convenience the skeleton is divided into regions: the axial skeleton, consisting of the skull and vertebral column; the visceral skeleton, including all parts of the gill bars; and the appendicular skeleton, consisting of the appendages and their girdles.

In primitive chordates without a skull, such as *Amphioxus*, the sense organs and central nervous system are of minor importance and have no protection other than the tissues surrounding them. As these structures around the mouth gain in importance to the animal, a skull is developed to enclose and protect them. The primitive skull, or chondrocranium, comes from the surrounding mesodermic tissues and is cartilage in the sharks and earlier vertebrates. *Amphioxus* has the notochord extending from the tip of the tail to the tip of the nose (Fig. 1), but in the higher forms the embryonic notochord extends only to the anterior end of the otic capsule.

Three sources have been used in skull building: (1) the chondrocranium, (2) the dermal plates or scales, and (3) parts of the visceral skeleton (Fig. 265). The neurocranium partly surrounds the brain and sense organs; the splanchnocranium is made up of added visceral elements. The dermocranium consists of membranous elements, added to complete the covering of the skull. The first real bone of the skull appears to have been the dermocranium, or membranous plates on the outside of the chondrocranium — a condition found in the sturgeons. This was followed by the ossification of the chondral structures beneath as in the teleosts.

A comparative study of the successive classes and their skulls shows a progressive series of developments, many of which have been made necessary by changes of function. The shift from water to land released a number of parts of both the skull and the visceral skeleton from their function of supporting the gills, and these elements became available building material to be modified and used for other purposes. The supporting apparatus of the gills became simplified as lungs developed. In tracing the history of the skull through the vertebrates, these changes will be considered in their proper place and sequence.

Fish Skull

The development of the primitive chondrocranium starts with the growth of bars of cartilage: the parachordals, a pair that parallel the notochord and extend one on either side to the anterior end of the otic capsules; and the trabeculae, a pair anterior to the parachordals and extending to the anterior ends of the eyes. Capsules of cartilage also surround the sense organs, the eyes, ears, and nose. By the coalescing of these cartilages, the chondrocranium is formed, the eyes remaining free. Sclerotic bones (Fig. 126 A) may develop around the eyes, but they are not joined with the skull except in a few birds (owls). Several occipital vertebrae are developed posterior to the otic capsules, varying in number and eventually fusing with the chondrocranium.

The skull of the sharks is a cartilaginous chondrocranium (Fig. 265) which serves as the permanent skull. The visceral arches have contributed the upper and lower jaws and their attachments to the skull (Figs. 264, 265). There are numerous openings in this chondrocranium, such as fontanelles and smaller foramina, passageways for nerves and blood vessels. These foramina persist throughout the vertebrates and are generally homologous. The future ossifications are fixed somewhat by these foramina as well as by points at which movement is necessary.

The chondrocranium of the shark is an irregular, plowshare-shaped mass of cartilage with numerous openings but with no sutures. The capsules of the nose and ears have joined with the rest of the mass, but the eyes remain free since they must be able to move. A median prolongation, the rostrum, with the two nasal capsules attached laterally at the base, marks the anterior end. The nasal cartilages are delicate and have openings for the nostrils. Posterior to the rostrum,
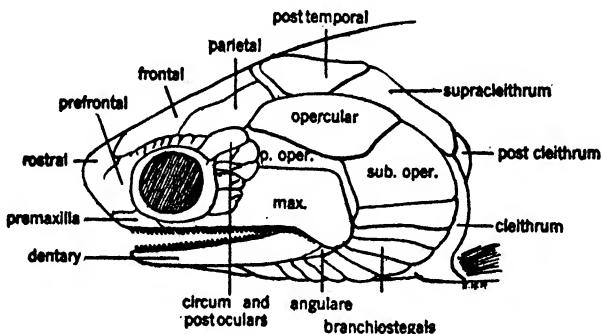
FIG. 69. Skull of Palaeoniscus. After Goodrich.
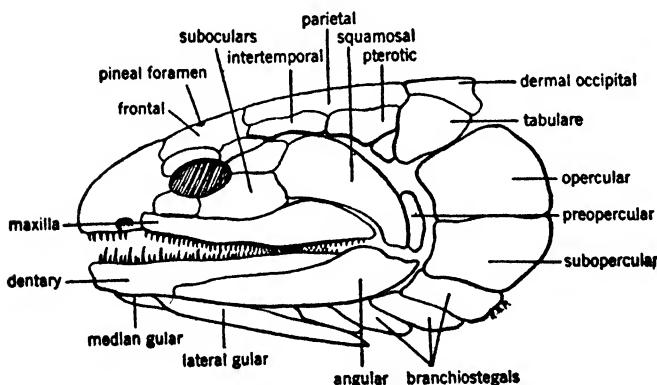
FIG. 70. Skull of Osteolepis. After Goodrich.

the cartilage extends out laterally to form the preorbital ridge, and a similar ridge is developed as the postorbital. The posterior end of the chondrocranium, which includes the otic capsules, is heavy and substantial. The ventral region is much narrower and more irregular with a keel on the ventral side of the rostrum. The region ventral to the brain is quite narrow between the otic capsules. The sella turcica, a depression on the floor of the chondrocranium into which the hypophysis projects, shows plainly from the ventral side, in its usual position

just posterior to the optic chiasma. The notochord shows as a light streak along the median line, extending forward to the anterior border of the otic capsules. The dorsal side of the chondrocranium has a pair of large anterior fontanelles formed by the trough-shaped rostrum, and ventrally, another pair of openings that lead to the brain cavity. The epiphyseal foramen for the pineal eye, which lies just posterior to the anterior fontanelles, is covered with a membrane.

Between the otic capsules is the endolymph fossa, into which the endolymph and perilymph ducts of the ears open. The foramen magnum, with its small condyle-like structures, marks the articulation with
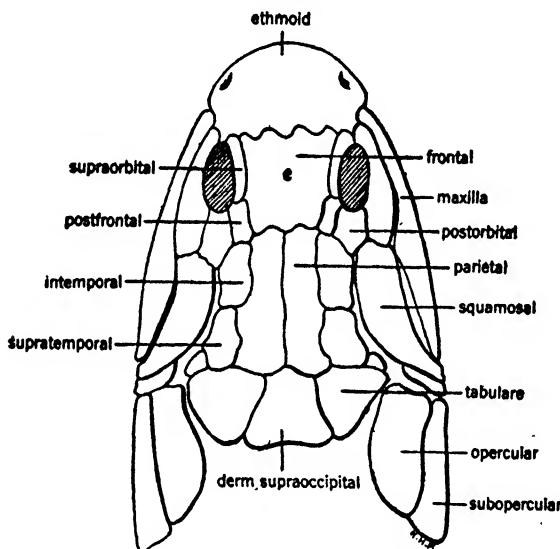
FIG. 71. Dorsal aspect of skull of Osteolepis. After Goodrich.

the vertebral column. Over the surface, at various points, are large and small foramina for nerves and blood vessels, those for the cranial nerves coming out laterally and ventrally. The chondrocranium of the shark encloses the brain and protects it from stresses and strains caused by the movements of the visceral skeleton. By the consolidation of the sense capsules with the rest of the skull, these parts receive additional protection.

The sturgeon (Fig. 74) retains the chondrocranium but also adds a number of dermal plates representing coalesced scales. The dermal skeleton may be peeled off like a glove, revealing the unossified chondrocranium beneath. The dermal plates are external and are usually sculptured, thus showing their superficial position. The lateral line can

be traced over these dermal elements by a series of small tunnels extending along its path. In higher fishes (Figs. 69, 70, 71, 75), the series of dermal plates join and assume definite positions, thus approaching the conditions found in the teleosts. This skull development may be
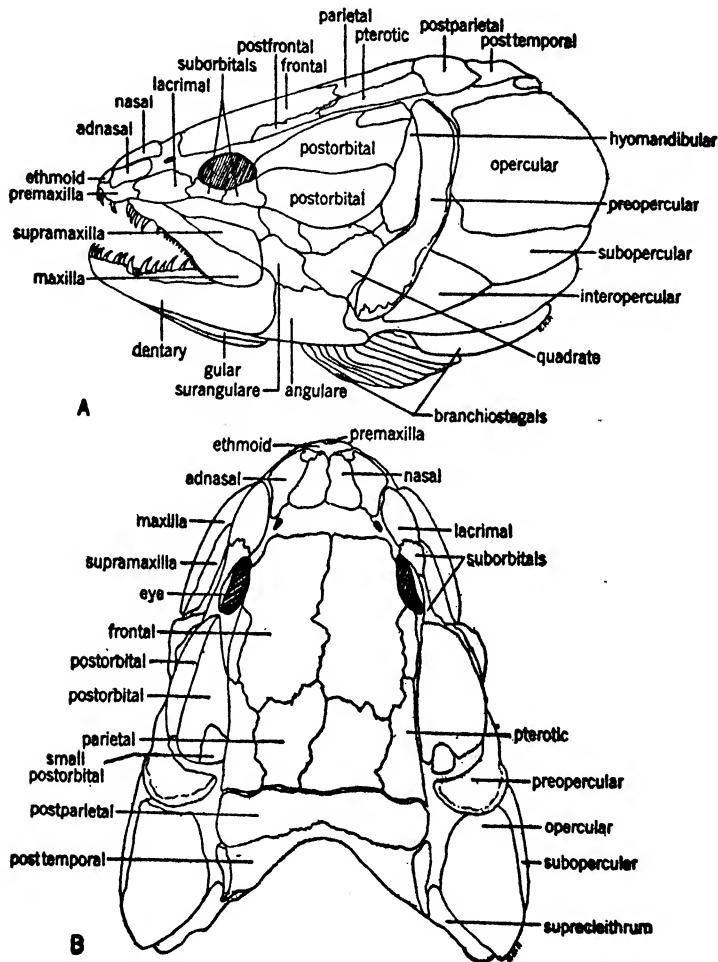
FIG. 72. Skull of Amia calva. A, lateral; B, dorsal.

traced through the intermediate series represented by fishes such as *Amia* (Fig. 72 *A, B*), *Lepisosteus* (Fig. 74 *A, B*), *Acipenser* (Fig. 74), and *Polypterus*. In these there are different stages of ossification of the chondrocranium, with a gradual sinking in of the dermal bones, until they finally join closely with the chondral bones to form the skull of the teleosts. The first ossifications are always found around the sense

organs and the foramina of the cranial nerves. `Low teleosts, such as the trout and salmon, retain much cartilage in the chondrocranium, but the higher teleosts have a well-ossified skull.

The skull of the carp (*Cyprinis carpio*) represents a very complete ossification of the chondrocranium as well as a close interlocking of the cartilaginous and dermal elements (Figs. 76, 77). The plan of the skull is fairly typical of that found in the teleosts, with the added ad-
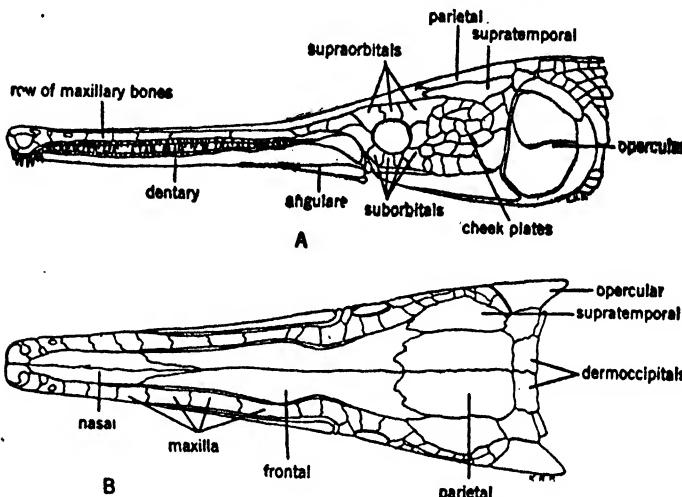
FIG. 73. Skull of Lepisosteus platostomus. A, lateral; B, dorsal. After Mayhew.
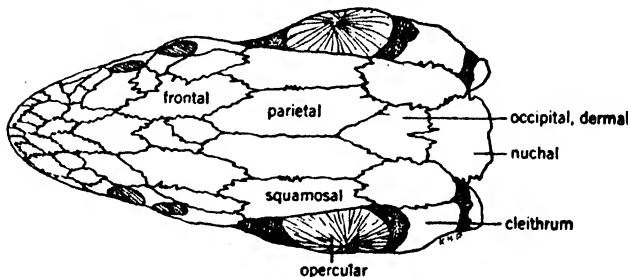
FIG. 74. Skull of Acipenser, dorsal aspect.

vantage that the bones are quite solid and have very definite outlines and plain sutural lines. The brain case and sense organs are completely covered by a well-knit series of bones that form the neurocranium. The foramen magnum is surrounded by four occipital bones, one being dorsal (the supraoccipital), two lateral (the exoccipitals), and a single ventral (the basioccipital). The ear is surrounded by two bones, the prootic and the epiotic, the opisthotic probably being joined to the prootic. The optic tract reaches the eye through a foramen in the

orbitosphenoid. Sclerotic plates develop around the eye, but are not connected with the skull. The lacrimal bone, in the anterior angle of the eye socket, merely represents the anterior element of the suborbital ring (Fig. 75), but it receives no duct from the eye. The nerves of the olfactory tract reach the nasal sacs through foramina in the ethmoid bone. The brain case is made up of the four occipital bones, the prootics, epiotics, alisphenoids, orbitosphenoids, and the single meseth- moid (Fig. 76 A). The floor is completed by the long dermal para- sphenoid, which extends almost the complete length of the skull (Fig. 76 B). The vomer is applied to the ventral surface of the parasphenoid at its anterior end. The roof is made up of the supraoccipital, prefrontals,
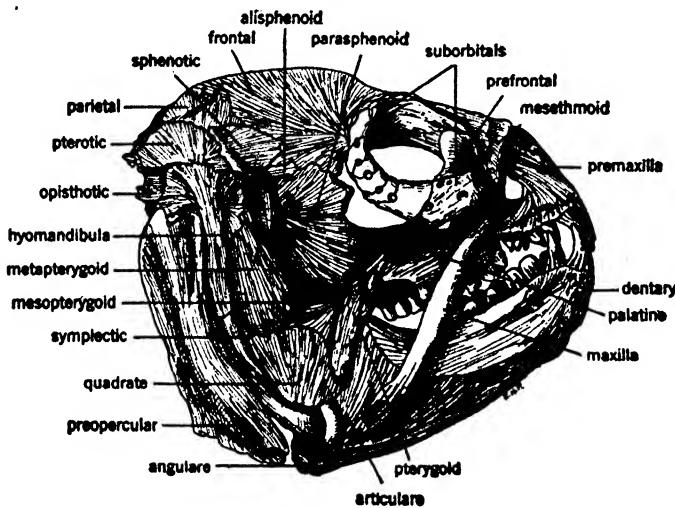
Fig. 75. Skull of Anarrhichthys ocellatus, lateral.

frontals, postfrontals, supraorbitals, pterotics, and the mesethmoid (Figs. 76, 77). The preethmoid extends from the mesethmoid to the premaxillae, which are not toothed in the carp. The key element of the jaw series is the quadrate, which is braced to the roof of the skull through the symplectic and the hyomandibular (Fig. 75), the latter articulating with the pterotic and postfrontal. The quadrate is braced to the anterior part of the skull through the pterygoids and palatines. The metaptery- goid (Fig. 77), a cartilage bone, fills in the gap between the quadrate and the hyomandibular, connecting with the palatines and filling in the pharyngeal region. A small ectopterygoid is developed on the external edge of the palatoquadrate bar. The mandible (Fig. 94 A), also toothless, consists of a dentary, a small angulare, and an ossified articulare (Fig. 266).

The opercular series, which covers the gill region, consists of four

bones, the opercular, preopercular, subopercular, and interopercular (Fig. 266). The opercular has a facet by which it articulates with the hyomandibular (Figs. 69, 70, 72).
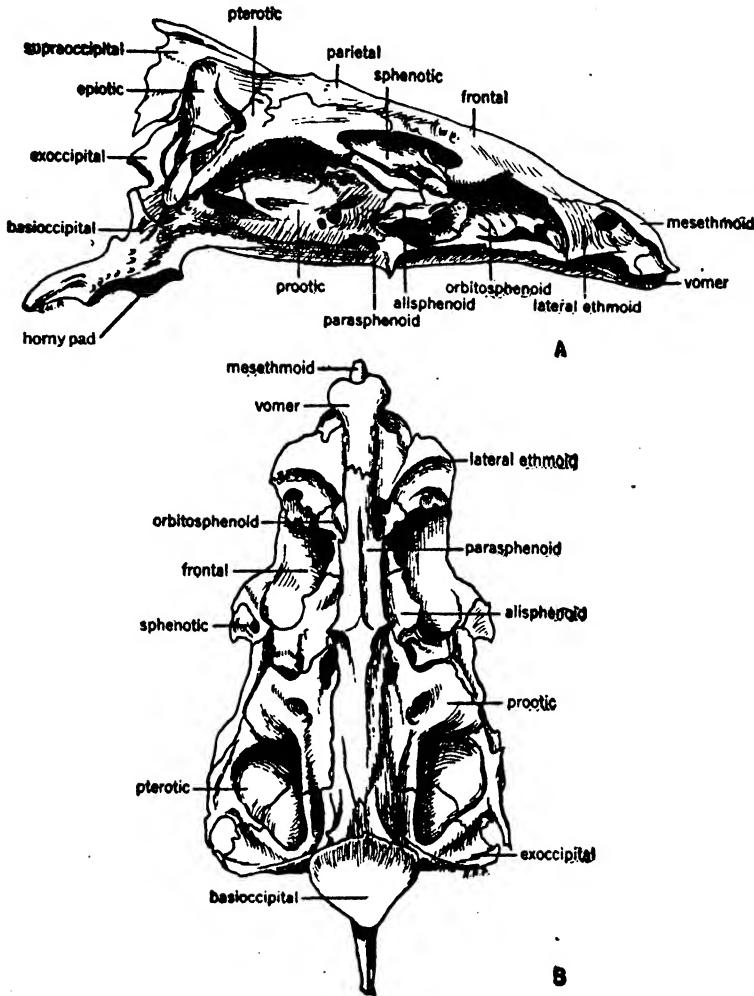
FIG. 76. Skull of carp with operculars and facial bones removed.
A, lateral; B, ventral.

The gills are connected with the skull through the hyal series consisting of the basi-, hypo-, cerato-, epi-, and interhyal (Fig. 264). The interhyal articulates with the hyomandibular, and the epihyal with the opercular. The urohyal, a modified branchiostegal, is a median bone articulating with the basihyal.

Each of the five gill bars, or branchials, consists of a number of elements: a basi-, hypo-, cerato-, epi-, and pharyngobranchial, the latter at the dorsal end of the arch. The fifth arch is modified, its pharyngeal
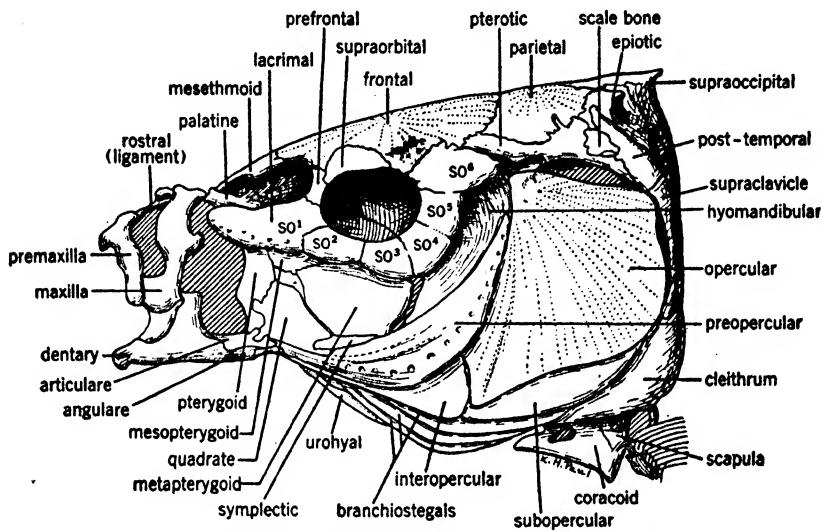
FIG. 77. Side view of carp skull, *Cyprinis carpio.* After Gregory.

element being enlarged and highly specialized and supplied with pharyngeal teeth, which are rubbed against a horny pad (Fig. 76 *A*), on the basioccipital.

Amphibian Skull

The skull of the Amphibia differs in a number of respects from that of the fish, because of anatomical changes associated with habitat shifts, that have made many of the fish elements unnecessary. A number of characters are retained that are inherited directly from the fishes, such as the lateral canals extending over the skulls. The organization of the skull of the stegocephalians is quite suggestive of that of the early intermediate forms to be found among the fossil crossopterygians, with solidly roofed crania and no openings except those for the sense organs and the pineal eye.

The bones of the cranium are greatly reduced in number in modern Amphibia (Figs. 79 *A*, *B*). The quadrate is no longer articulated to the skull through the symplectic and hyomandibular, but through the squamosal. The hyomandibular has become the stapes, and the symplectic the columella. The skull is platybasic (flattened), and the parachordals, a pair of cartilaginous bars, paralleling the notochord in

early development, meet in the region of the ethmoid plate. This in contrast to the reptilian skull, in which the parachordals meet in the region of the hypophysis. The two occipital condyles are formed by the exoccipitals. The neurocranium is quite narrow in the frog, being about one-sixth of the total width of the skull (Fig. 79 *A*, *B*). The foramen magnum is surrounded by the exoccipitals, as the other occipital bones are not ossified. Since so much of the chondrocranium is retained, the brain is surrounded mostly by cartilage. The nose is in a nasal capsule, having a septomaxillary developed in connection with it and also an external nasal bone. The orbitosphenoid is not ossified, and the optic nerve extends through a foramen piercing the cartilage (Fig. 78). The ear elements are peculiar in that only the prootic is
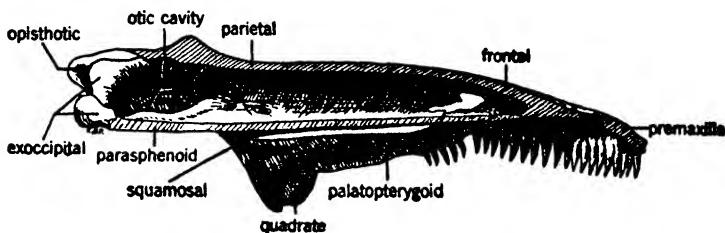
FIG. 78.   Skull of Necturus, sagittal section.

present as a separate bone. The stapes (Fig. 79 *B*) is well developed, with its base in position in the foramen vestibuli and its columella in contact with the tympanum, which is supported by the cartilaginous annulus tympanicus (Fig. 79 *A*). (See Chapter X.)

The roof of the skull (Fig. 79 *A*) consists of the frontoparietals, the nasals, and the ethmoids, with the prootics and sphenethmoids as side walls. The ventral part of the brain case is made up of the dagger-shaped parasphenoid and the triangular vomers, both of which are dermal bones. The splanchnocranium is extensive, and its outline gives width to the skull. The premaxilla, maxilla, and quadratojugal form the arc that extends to the quadrate. A large pterygoid forms the second brace for the arc, connecting with the palatine anteriorly and the prootic posteriorly. The vomer, premaxilla, and maxilla are toothed in *Rana*.

The mandibular cartilage extends out from the dentary, forming the mento-Meckelian cartilages. The bones of the mandible are the dentaries, articulars, and angulars, only the dentary being toothed (Fig. 79 *C*).

The visceral skeleton is much reduced in *Rana* but is more extensive in water forms, such as *Necturus* (Fig. 97 *A*) and *Cryptobranchus*. The
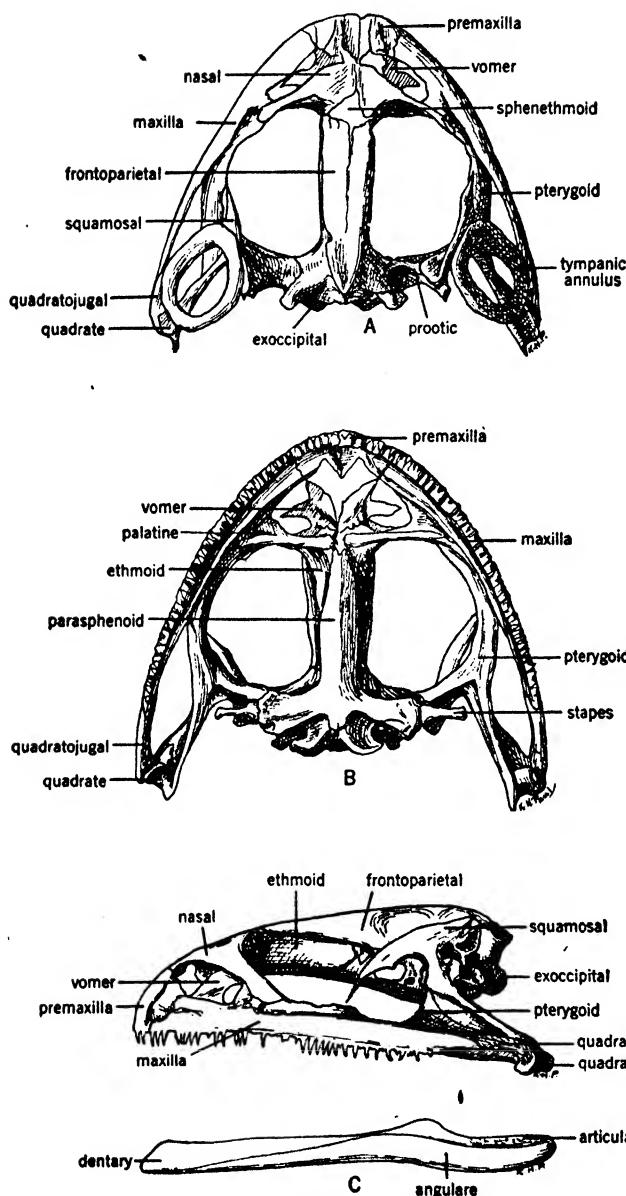
FIG. 79. Three views of the skull of Rana catesbeiana (bullfrog) A, dorsal; B, ventral; C, lateral.
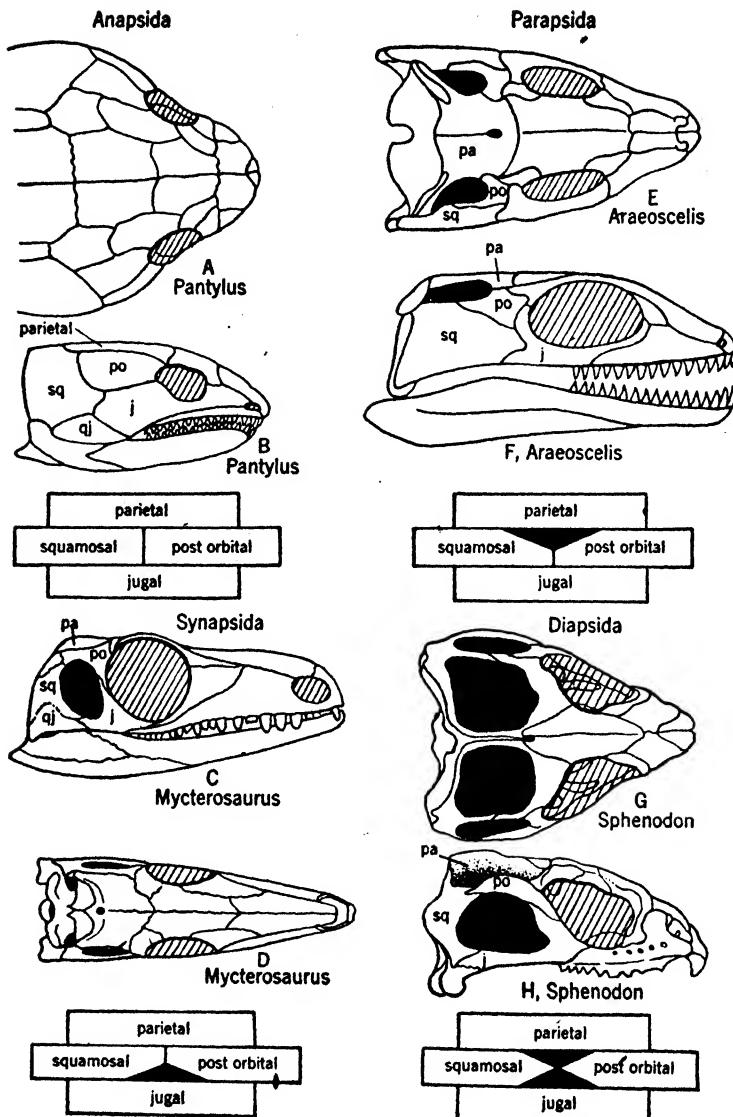
Fig. 80. Diagram showing the relation of the temporal openings in the reptilia. The small diagrammatic figures beneath the skulls show the relation of the skull bones to these openings. A and B, Pantylus; C, Mycterosaurus; D, Mycterosaurus; E and F, Araeoscelis; G and H, Sphenodon.

body of the hyoid is a cartilaginous plate formed by the fusion of the central parts.

In urodeles, the skull is usually more substantial in structure than in the Anura, being more compact and having fewer fontanelles (Fig. 78). The maxillary arch is broken, as no jugal is present and the pterygoid no longer reaches the palatine.

Reptilian Skull

The skulls of modern reptiles are easily differentiated from those of the amphibians, but those of primitive reptiles and primitive amphibians are not so easily separated. Whereas modern reptiles are characterized by having a single condyle, the fossil Therapsida (Fig. 83) had two, as do the amphibians and mammals. The condition of the palate serves to separate modern reptiles and amphibians but not the older forms. In modern reptiles, the tropibasic condition of the skull is perhaps one of the most striking features, since the trabeculae join
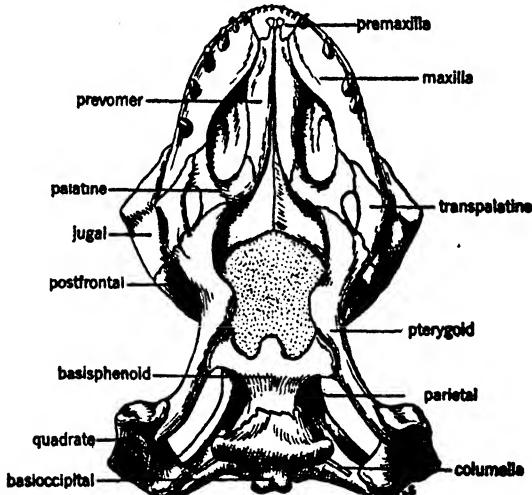
Fig. 81.   Skull of Heloderma.   Ventral.

each other in the region between the eyes, so that the skull is high rather than flat. Reptiles have a number of elements that do not appear in modern amphibians, such as the transpalatines and epipterygoids; and the parasphenoids (Fig. 81), so characteristic of both the fishes and amphibians, become small or vestigial. Some reptiles, particularly the turtles (Fig. 84), have a very heavy skull with bones closely joined, and the quadrate firmly fixed, a condition called monimostylic; others have lighter skulls in which the bones are not so closely

joined and movement of the quadrate is possible, a condition known as streptostylic. Snakes and many lizards show this condition of a free quadrate. The skull of the reptiles is a much better mechanical structure than that of the amphibians. All traces of the lateral line are lost, and there is a freer movement of the skull on the atlas because of the type of condyle and improved cervical vertebra.

, The classification of the reptiles is based largely on skull characters, starting with the early cotylosaurs, in which the roof has no openings besides those for the sense organs, and ending with the lizards and *Sphenodon*, in which there are numerous fenestrations (Fig. 80).

Anapsidan Skull. — The typical anapsidan skull (Fig. 80 *A, B*) is found in primitive reptiles known as cotylosaurs. In *Seymouria baylorensis* (Fig. 82 *A, B*), one of the earliest forms, the skull roof is not fenestrated. The roofing bones consist of dermoccipitals, parietals, frontals, and nasals with a pineal foramen between the parietals. Laterally, the roofing is filled in by the epiotics (tabulare) supratemporals, intertemporals, postfrontals, prefrontals, and lacrimals. Laterally the skull is completed by the squamosals, quadratojugals, jugals, maxillae, and premaxillae. A notch permits the stapes to reach the tympanic membrane.

Synapsidan Skull. — The Synapsida are ancient forms, with few modern representatives except the mammals, now considered as descendants. The condition of the skull has been changed by the opening of a fenestra on the side of the skull, between the postorbital, squamosal and jugal (Fig. 80 *C, D*). The fenestra varies from a small slit to a large fossa. Among the Therapsida (Fig. 83), mammal-like reptiles, there is a close approach to the mammalian type of skull with heterodont dentition and two condyles. The reduction of the bones of the jaw region is suggested by the conditions found in such forms as *Cynognathus* (Fig. 80 *C, D*), where the dentaries were greatly enlarged and had a process approaching the squamosal to form a new contact and a new mandibular condyle. The posterior mandibular elements were becoming reduced in size. The jugal and squamosal formed an arch, the teeth were in sockets, a secondary palate was being formed, there was a long external auditory meatus, and the quadrate was becoming quite small.

In turtles (Chelonia) the skull (Fig. 84) appears to be of the anapsidan type, although some of the land turtles approach the conditions found in the Synapsida. It is possible that the Chelonia have a secondary roof which resembles that of the cotylosaurs, although the condition may not be primitive but secondary. The greatest extreme is reached in the land turtles, where the emargination of the roof has an entirely

different appearance, with the postorbital bar similar to that of the Synapsida, and for this reason they are included with them.

Forms other than sea-turtles show a specialization of the bones around the quadrate region by which a resonance chamber is developed.   In
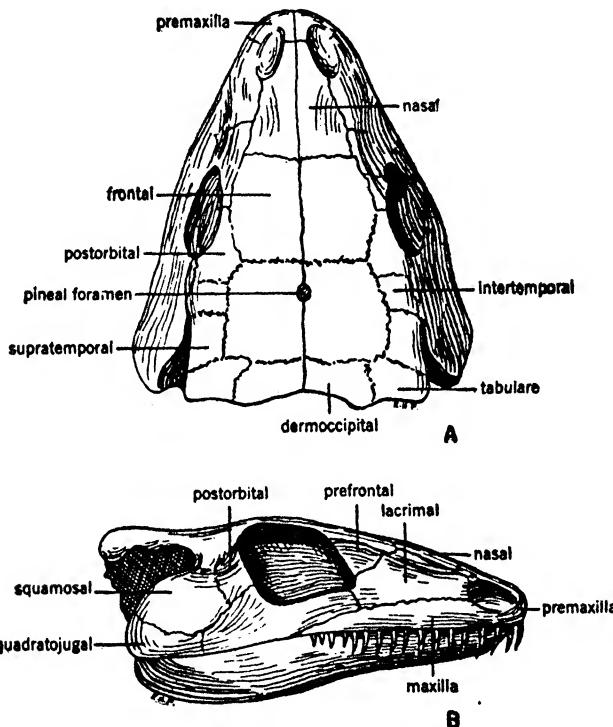
FIG. 82.   Skull of Seymouria.   A, dorsal; B, lateral.

Amyda, the squamosal is hollowed out to form a thin-walled chamber in connection with the tympanum.   The stapes is able to reach the tympanum through a notch in the quadrate.

Parapsidan Skull. — The lizards and snakes are modern representatives of the Parapsida (Fig. 80 *E, F*).   The skull of the lacertilians is usually very light and of the streptostylic type with a movable quadrate. The bones are not strongly articulated, and some of them are capable of slight movement.   The Squamata, including the lizards and snakes, belong in the Parapsida since they have only one temporal arch formed by the jugal and the squamosal, and even that is not always complete. They generally have a posttemporal arcade.

In the lizard *Heloderma* (Fig. 81), the skull is roofed over by the parietals, frontals, post- and prefrontals, nasals, and lacrimals.   The

lateral series of the roof are the premaxilla, maxilla, jugal, and the squamosal and quadrate. The base of the skull is typically lacertilian, the median series consisting of the basioccipital, basisphenoid, a carti-laginous parasphenoid, pterygoid, transpalatine, epipterygoid, palatines and prevomer. The condyle is formed by the basioccipital for the most part, since the exoccipi-tals enter but slightly into its structure. The otic series, all being joined with the exoc-cipitals and other bones of the region, are not evident as separate ele-ments. The long thin stapes extend to the tympanum stretched in the otic notch of the quadrate. The gap between the brain case and the anterior part of the skull is filled by a cartilaginous wall representing the unossified alisphenoids.

FIG. 83. Skull of Ictidopsis.

In the snakes the skull is more specialized than in the lizards and its
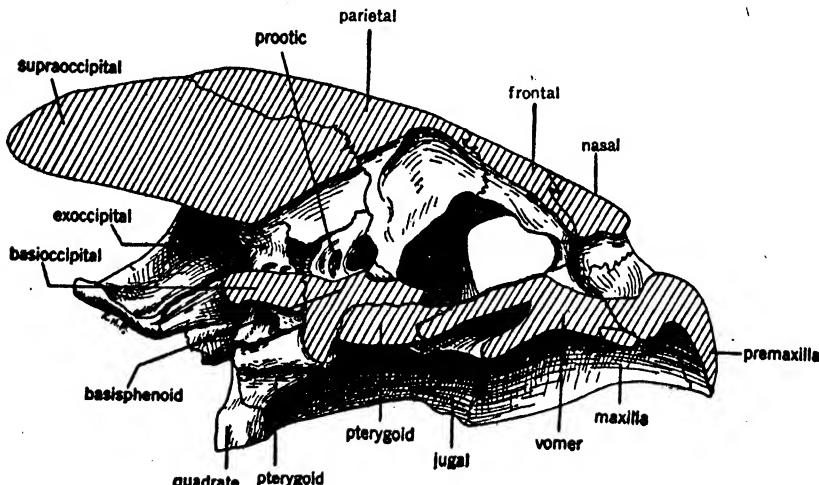
FIG. 84. Skull of sea-turtle (Thalassochelys caretta). Sagittal section.

streptostylism is more pronounced, since all the elements except those of the brain case are movable. The articulations are of the loose, contact type so that the greatest freedom of movement is obtained. The quadrate extends posteriorly and is joined to the skull by the squamosal. The jugals and epipterygoids have been lost, and the orbito- and alisphenoids usually ossify. The bones of the mid-dorsal

line are the supraoccipital, parietals, frontals, nasals, and premaxillae. The brain case is formed by the ventral extensions of the frontals and parietals, which form the dorsal walls and a part of the sides, with the prootics, exoccipitals, basioccipital, and basisphenoid completing the structure. The squamosal is not included in the brain case. The premaxillae, maxillae, palatines, transpalatines, pterygoids, and dentaries have teeth. The stapes extends from the fenestra vestibuli to the quadrate, since no tympanum is present. The peculiarities of the snake skull are due to the use made of these elements in food swallowing. The pterygoid, attached to the movable quadrate, forms a part of the series consisting of the pterygoids, transpalatines, palatines, and maxillae. All these permit a maximum of movement and the independent use of the two sides, the series acting as levers to pull the' food down into the throat. They are assisted by the two mandibles working separately with an antero-posterior movement.

Diapsidan Skull. — The Rhynchocephalia, of which *Sphenodon* (Fig. 80 *G*, *H*) is the only living representative, is most striking in its skull architecture, since it has two temporal arcades and a posttemporal fossa. There were numerous representatives of this type among the ancient reptiles.

Avian Skull

The skull of birds is very light and pneumatic, resembling that of pterodactyls, in some respects, with a tendency for all the individual elements to fuse into one piece, except the quadrates, which remain free and movable (Fig. 306). Teeth, the absence of which separate the birds from the modern reptiles, were present in *Archaeopteryx, Hesperornis,* and *Ichthyornis.* Modern birds have the jaws encased in a horny beak, resembling that of the turtles.

The skull is tropibasic and, since the quadrate is free, is streptostylic. The brain case is large, a feature that also separates the birds from the reptiles. The foramen magnum is inclined ventrally, and in owls and hawks its position is clearly ventral. The occipital condyle is formed by the basioccipital. There is much variation in the base of the skull and in the formation of the palate, so much so that it has been used in separating the different groups of birds. The skull is fused in the adult so that the separate bones are not distinguishable, and young forms must be studied to separate the skull elements.

Mammalian Skull

In mammals the skull differs from that of other vertebrates by having a larger brain case, double condyles, heterodont dentition, with teeth

only on the premaxillae, maxillae, and mandibles (Fig. 85). Reptilian
bones not appearing in the mammals are the prefrontals, postfrontals,
epipterygoids, transpalatines, supraorbitals, and quadratojugals; and
it is probable that the alisphenoid is not homologous with the bone of
the same name in the reptiles. There also seems to be a difference in
the origin of the vomer of mammals, and it is probable that there may
be either a vomer or a prevomer.

The posttemporal fossa is not present in the mammals, except in the
monotremes. The two condyles are formed by the exoccipitals as in
the amphibians. The sphenoids tend to combine and form one ele-
ment, and in the temporal region the following bones are closely asso-
ciated and may be combined to form one structure: pterotic, prootic,
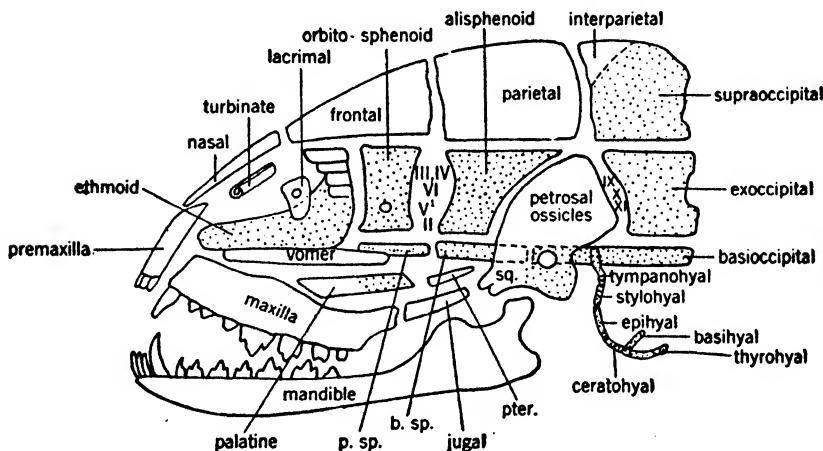
Fig. 85. Diagram of mammalian skull, cartilage bones stippled, dermal bones
white. Redrawn from Weber.

epiotic, opisthotic, squamosal, tympanic, stapes, incus, and malleus.
The squamosal forms the new articulation for the mandible. There
are three ossicles (Fig. 226): the stapes, derived from the hyomandibu-
lar; the incus, derived from the quadrate; and the malleus, generally
thought to be the articulare. The mandible consists of a pair of bones,
the dentaries.

The importance of a number of reptilian elements is lessened con-
siderably in the mammals because of the new architecture and the
great enlargement of the brain case. The brain case is now com-
pletely enclosed, the ethmoids forming a cribiform plate at the anterior
end, for the twigs from the olfactory tract. The occipitals, ankylosed
into one piece, form the posterior wall; the parietals, temporals, and

frontals form the roof and most of the sides; the rest is filled out by the orbito- and alisphenoids (Fig. 88). The floor is formed by the occipital, basisphenoid, presphenoid, and temporal, together with the two lateral bones, the orbito- and alisphenoid (Fig. 90). The greatest
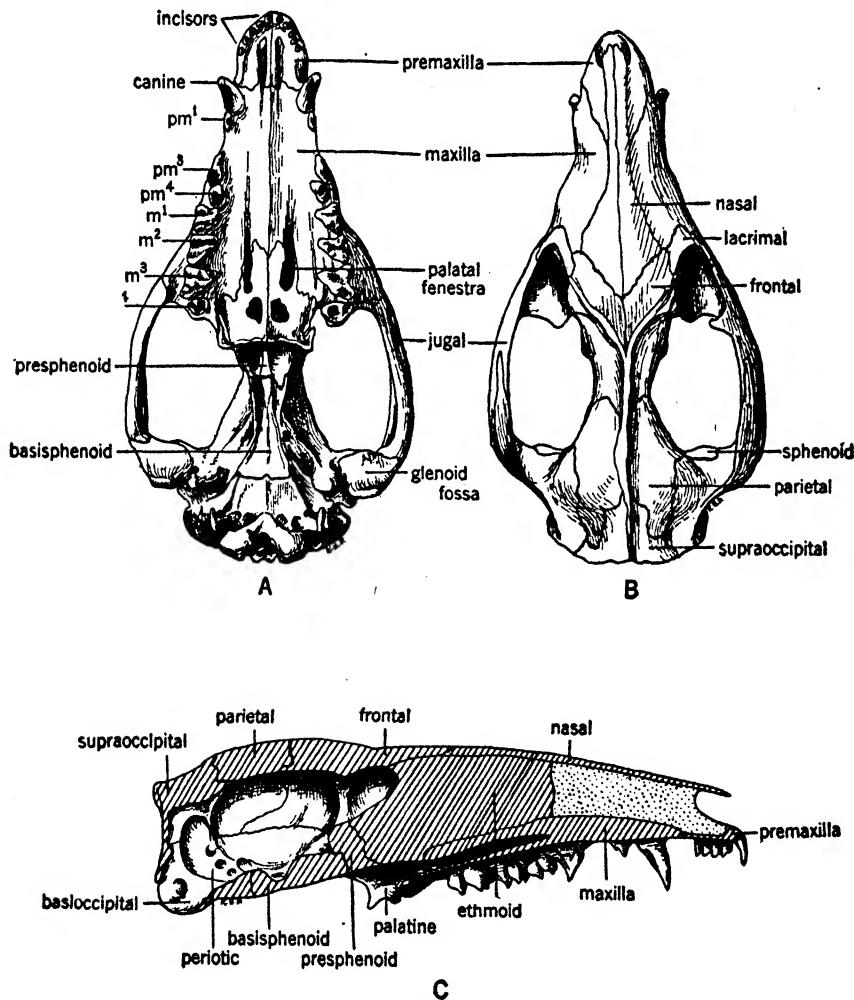
FIG. 86. Skull of opossum (Didelphis). A, ventral; B, dorsal; C, sagittal.

change in the basicranial region comes because of the shift of the quadrate into the ear. The quadrate in all other groups has been the center for the articulation of elements connected with the palate; and with its loss, this series loses its importance. The temporal depends on its articulation with the brain case for its bracing, which makes it secure
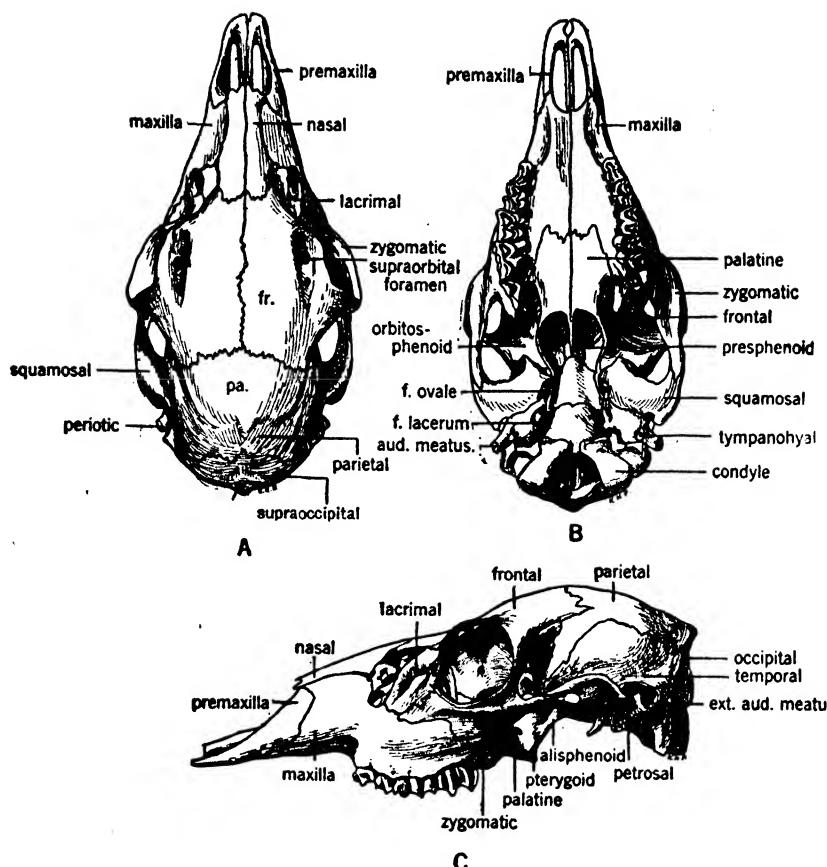
FIG. 87. Skull of mule deer (Odocoileus). A, dorsal; B, ventral; C, lateral.
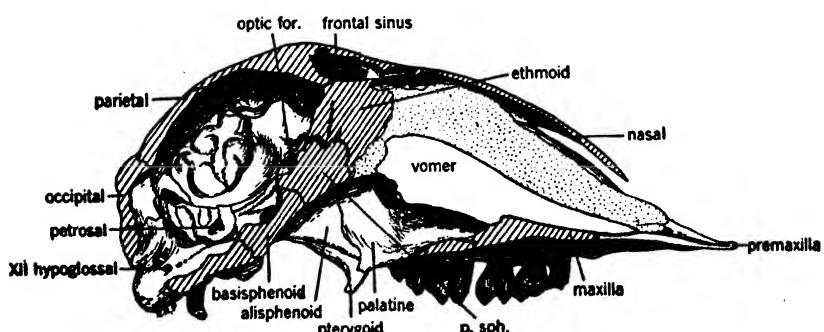
FIG. 88. Skull of domestic sheep, sagittal section.
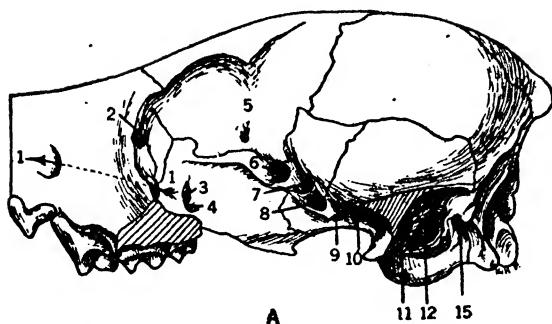
FIG. 89. Skull of dog showing lateral foramina. (With table of foramina.)
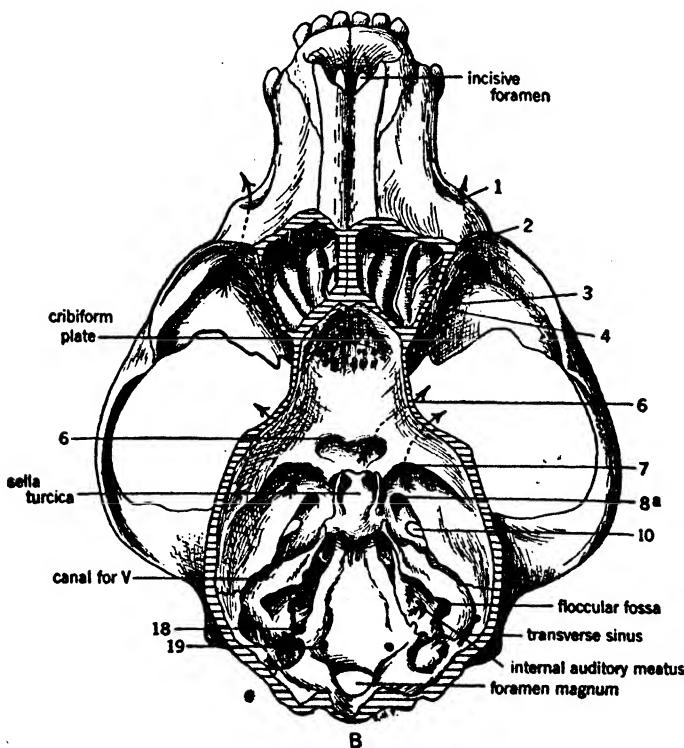
FIG. 90. Skull of dog with cranial roof removed to show foramina. (With table of foramina.)

and removes the need for outside supports. The jugal is extremely important as a brace for the maxillae, especially in forms with great stress on the molars, as in carnivores. The pterygoids and palatines no longer serve as braces. The pterygoids become vestigial or serve merely for the insertion of small pterygoid muscles. The palatines,
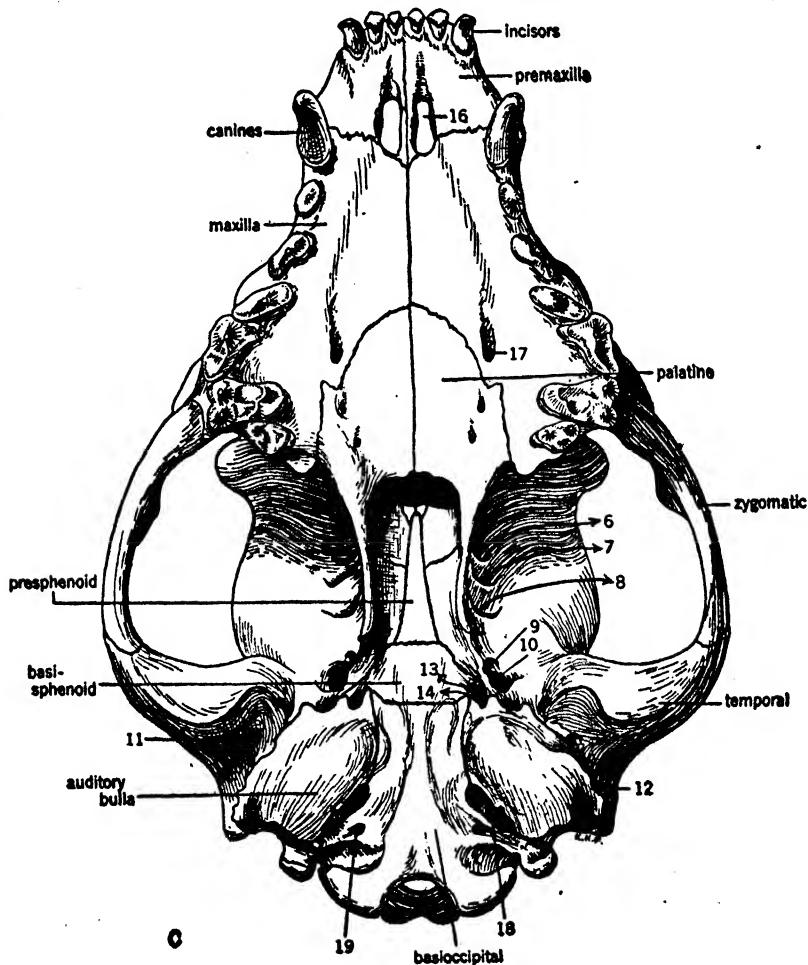
FIG. 91. Skull of dog, ventral, to show foramina. (With table of foramina.)

together with the maxillae, form a secondary shelf, the hard palate, ventral to the old mouth roof. This new palate (Figs. 86 *A*, 87 *B*, 91) is suggested in the alligators, where the nares are far back because of the mesial growth of the maxillae.

Although the skulls of all mammals show a general similarity, some

striking differences separate the monotremes, marsupials, and pla-
cental mammals.   The monotremes retain a number of reptilian char-
acters not found in the more advanced mammals, such as a posttemporal
arcade and a prevomer, or dumbbell bone.   The palatines and ptery-
goids enter into the formation of the brain case, a condition not found
in the higher mammalian groups.   The marsupials have a fenestrated
palate (Fig. 86 *A*), an inflected angle on the mandibles, and a brain
case of comparatively small size.   The dentition (Fig. 86 *A*) of the
marsupials is sufficient to distinguish them from the placentals.   In
placental mammals, the brain case is greatly enlarged, the characters of
the marsupials are lacking, and the dentition is very different.   The
brain case becomes progressively larger in the placentals (Figs. 86 *C*,
88), with a corresponding reduction in the size of the facial elements,
until in the primates the brain case makes up most of the skull.
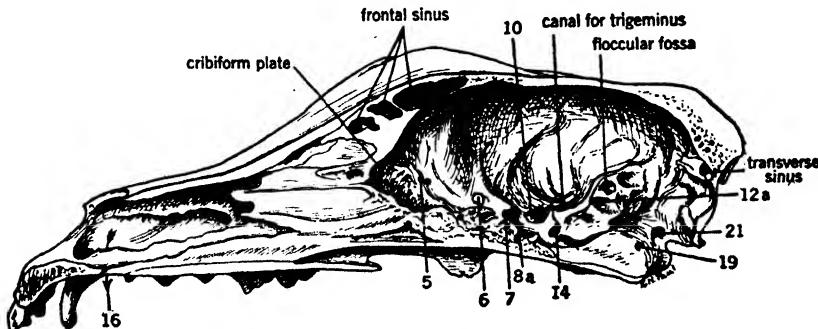
FIG. 92.   Sagittal section of dog skull, showing foramina.

The roof of the mammalian skull (Figs. 86 *B*, 87 *A*) is left fairly
intact with only a few small openings for twigs of nerves and blood
vessels, but the sides and the floor are pierced by numerous openings,
through which the cranial nerves and blood vessels may either enter or
escape from the skull.   Although a number of foramina and openings
are formed on the lateral side, it is on the ventral face that most of them
appear (Figs. 89, 90, 91, 92).

Cranial foramina are for the most part surprisingly uniform in the
class Mammalia.   A few are variable and may be confluent with some
other foramen or missing entirely.   They are very useful in classifi-
cation, since the presence or absence of certain foramina differentiates
orders very clearly.   The general position of the foramina is practically
fixed early in the history of the tetrapods, and subsequent changes
are related to changes in the structures that extend through the skull
or in the skull itself.   The foramina and openings of the skull are of

FORAMINA OF THE DOG SKULL

Foramen	Bones concerned	Structure transmitted
1. Infraorbital canal	Maxilla	V^2 branch of V
2. Lacrimal	Lacrimal bone	Naso-lacrimal duct
3. Sphenopalatine	Palatine	Sphenopalatine nerve and artery
4. Posterior palatine	Palatine	Palatine nerve and artery
5. Ethmoid	Frontal	Ethmoid branch of V^1
6. Optic	Orbitosphenoid	Optic tract
7. Sphenoidal	Between orbito-, ali-, and basisphenoid	Nerves III, IV, V^1, VI
8. Anterior pterygoid	Ali- and basisphenoid	Maxillary branch or V^2
8ª. Rotundum	Basisphenoid	Maxillary branch or V^2 outlet of external carotid
9. Posterior pterygoid	Alisphenoid	External carotid
10. Ovale	Alisphenoid	V^3 of trigeminus
11. Posterior glenoid	Squamous portion of temporal	Vein from the transverse sinus of meninges
12. External auditory meatus	Bulla of temporal	Inlet to tympanum of ear
12ª. Internal auditory meatus	Petrous portion of temporal	Nerves VII and VIII
13. Eustachian	Between bulla and ali-sphenoid	Tuba auditiva
14. Carotid	Through temporal ventral to bulla	Loop of the internal carotid extends into this foramen
15. Stylomastoid	Between temporal and basioccipital	Exit of VII
16. Incisive	Between maxilla and premaxilla	Connects with Jacobson's organ, transmits naso-palatine nerve, Stenson's duct, and palatine nerve
17. Anterior palatine	Between maxilla and palatine	Palatine nerve
18. Posterior lacerum	Between bulla and basioccipital	Nerves IX, X, XI, internal carotid, veins from the meningeal sinus
19. Hypoglossal	Occipital bone	Nerve XII
20. Foramen magnum	Occipital bone	Spinal cord, veins and arteries from brain case
21. Condylar canal	Occipital bone	Condylar vein from meninges
22. Mandibular	Mandible	V^3 and blood vessels
23. Mental	Mandible	Branch of V^3 to chin and blood vessels

course fixed at an early period of development, so that the vessels and nerves establish their position before the bones and definite outline materials are formed. The vessels and nerves appear first, and the bones either form around them or the vessels are left between sutures. There are numerous small foramina that are not stable but subject to much variation both in position and size, that transmit small nerves or blood vessels. The parietal foramen present in some mammals is not common in the dog.

Skull Foramina

1. Infraorbital. — This foramen is constant in mammals, but is quite variable in shape and size. It is quite large in rodents, since a part of the origin of the masseter muscle extends into its cavity. It transmits the maxillary branch of the trigeminus nerve (V^2) and some blood vessels. (Figs. 89, 90.)

2. Lacrimal. — The lacrimal bone is usually pierced by the naso-lacrimal duct which connects the corner of the eye with the nasal cavity. It is lacking in pinnepeds and a few other orders. (Figs. 89, 90.)

3. Sphenopalatine. — The foramen is on the lateral face of the palatine bone, and is the more dorsal of two small openings in this region. It transmits the sphenopalatine nerve, a branch of V^2, and an artery to the nasal cavity. (Figs. 89, 90.)

4. Posterior Palatine. — The foramen is ventral to the sphenopalatine and extends through to the anterior palatine foramen which is its outlet to the palate (foramen 17). It transmits the palatine nerve (a twig from V^2) and a small artery. (Figs. 89, 90.)

5. Ethmoid. — A small foramen on the side of the orbit, on the fronto-sphenoid suture. Transmits a branch of the palatine nerve, a twig of V^1, and is fairly constant in mammals. (Figs. 89, 92.)

6. Optic. — A constant foramen in mammals, that usually pierces the orbitosphenoid bone, although originally it probably came through the foramen lacerum anterior. It transmits the optic tract. (Figs. 89, 90, 91, 92.)

7. Sphenoidal. — The sphenoidal is the second of the three main foramina which, in the dog, either pierces the orbitosphenoid or is formed along its lateral border. Its position is really between the orbitosphenoid and the alisphenoid. In some animals it is confluent with the optic foramen (marsupials). It transmits nerves oculomotor, trochlear, a branch of the trigeminus (V^1), abducens, and may carry an additional branch of the trigeminus (V^2). (Figs. 89, 90, 91, 92.)

8. Anterior Pterygoid. — This foramen pierces the alisphenoid bone and is the third, in the row along the sides of the alisphenoid and orbitosphenoid, in the dog skull. It is confluent with the opening of the foramen rotundum (8^a), so that it is not clearly visible from the outside of the skull, since the flange of bone that forms the carotid canal somewhat covers it. The external carotid of the dog is enclosed in bone, and the anterior pterygoid is its outlet. This canal, known as the alar or alisphenoid canal, is present in many mammals, but lacking in monotremes, marsupials, artiodactyls, and others. (Figs. 89, 90, 91, 92.)

8ª. Foramen Rotundum. — This foramen pierces the sphenoid bone between the basisphenoid and the alisphenoid, and transmits a branch of V². (Fig. 92.)

9. Posterior Pterygoid. — The foramen is confluent with the opening of the foramen ovale (the pterygoid canal, taken up under 8, is the canal formed by a flange from the alisphenoid bone that extends dorsally, forming a canal for the external carotid). (Figs. 89, 91.)

10. Foramen Ovale. — This foramen, which is lateral to the glenoid fossa in the dog, is large and distinct. The entrance to the carotid canal is just mesial to it. Ovale transmits the mandibular branch of the trigeminus (V³), and is in a position so that the nerve can easily descend and reach the mandibular foramen on the inner side of the jaw. (Figs. 89, 91.)

11. Posterior Glenoid. — Lateral to the bulla and posterior to the prominent glenoid process, this foramen is large and well differentiated in the dog. It transmits a vein from the transverse sinus to the brain case. (Figs. 89, 91.)

12. External Auditory Meatus. — This large opening on the lateral side of the bulla leads to the tympanic membrane of the ear. The opening is prominent in mammals with an inflated bulla, but may be at the end of a bony tube in animals having a heavy, flat bulla. (Fig. 89; sheep, Fig. 87.)

12ª. Internal Auditory Meatus. — At about the middle point of the mesial face of the petrosal bone, a deep foramen transmits the auditory (VIII) and the facialis (VII). (Fig. 92.)

13. Eustachian (Tuba Auditiva). — The antero-mesial wall of the tympanic bulla ends in a rough, serrated edge, through which two openings appear in the dog. The more lateral of the two openings, with rough edges, is the Eustachian, through which extends the tuba auditiva or Eustachian tube. The more mesial opening is the carotid foramen. (Figs. 91, 92.)

14. Carotid Foramen. — This is mesial to the Eustachian tube opening, and is anterior to the auditory bulla. Its outline is smooth compared to the opening of the Eustachian tube. A loop of the internal carotid extends down into this foramen, but does not go through, since the loop returns to the skull cavity, immediately after making the loop, to supply the meninges and the brain. (Figs. 91, 92.)

15. Stylomastoid. — This is a small foramen at the posterior-mesial edge of the bulla, anterior to the large ventral process of the basioccipital. It transmits the facial nerve (VII) to the outside of the skull. (Fig. 89.)

16. Incisive. (Anterior palatine of some authors.) These foramina are large and distinct in the dog, their borders being formed by the

premaxilla and maxilla. In some animals they are almost confluent. They transmit the naso-palatine nerve (a branch of V²), Stenson's duct, and connect with Jacobson's organ. (Figs. 90, 91, 92.)

17. Anterior Palatine. — This foramen is on the roof of the mouth, lateral to the midline, and lies between the maxilla and the palatine. (There are often one or more other small foramina in this region, but they are small and irregular.) The foramen transmits an artery, which goes through to the floor of the nasal passage. (Figs. 91, 92.)

18. Posterior Lacerum. — This foramen is the large, irregular opening, between the posterior face of the auditory bulla and the basioccipital. It transmits cranial nerves, glossopharyngeal, vagus, spinal accessory, and a large vein from the transverse sinus, and it is the entrance of the internal carotid to the brain case of the skull. (Figs. 90, 91.)

19. Hypoglossal. — This nicely formed round foramen is just posterior to the posterior lacerum (18). It pierces the basioccipital bone and transmits cranial nerve hypoglossal (XII). (Figs. 90, 91, 92.)

20. Foramen Magnum. — This, the largest foramen of the skull, is surrounded by the occipital bone. It transmits the spinal cord, and arteries and veins connected with the brain case. (Fig. 90.)

21. Condylar Canal. — This large foramen, in the lateral wall of the foramen magnum, transmits a large vein from the brain sinuses. (Fig. 92.)

22. Mandibular Foramen. — This large foramen is on the inner side of the mandible, just anterior to the condyle. It transmits the mandibular branch of the trigeminus (V³), and blood vessels to the teeth and the inner region of the mandible. A part of this nerve extends through the mandible and comes out again at the mental foramina to continue as the mental nerve.

23. Mental Foramen. — This opening is on the lateral side of the mandible and usually ventral to the first or second premolar. Often smaller foramina appear in this region of the jaw. The foramen transmits the mental nerve, a branch of V³, and blood vessels. (Fig. 96 B.)

Visceral Skeleton

The origin of the lower jaw goes back to the shark stage of the chondrocranium and the use of the visceral arches. The original jaw is considered as a visceral arch modified to form the Meckelian and palatoquadrate cartilages; just posterior to it, the hyoid arch forms a suspensory apparatus. The attachment of the jaw to the skull is made in three different ways. In the most primitive sharks, the attachment

is amphistylic (Fig. 93 *A*), both the mandibular and the hyoid arches being firmly attached to the skull.

The hyostylic attachment (Fig. 93 *B*), present in *Squalus*, is formed by both the mandibular and hyoid arches being attached to the chondro-cranium by ligaments, the hyoid being functional in the support of the mandibular cartilages.
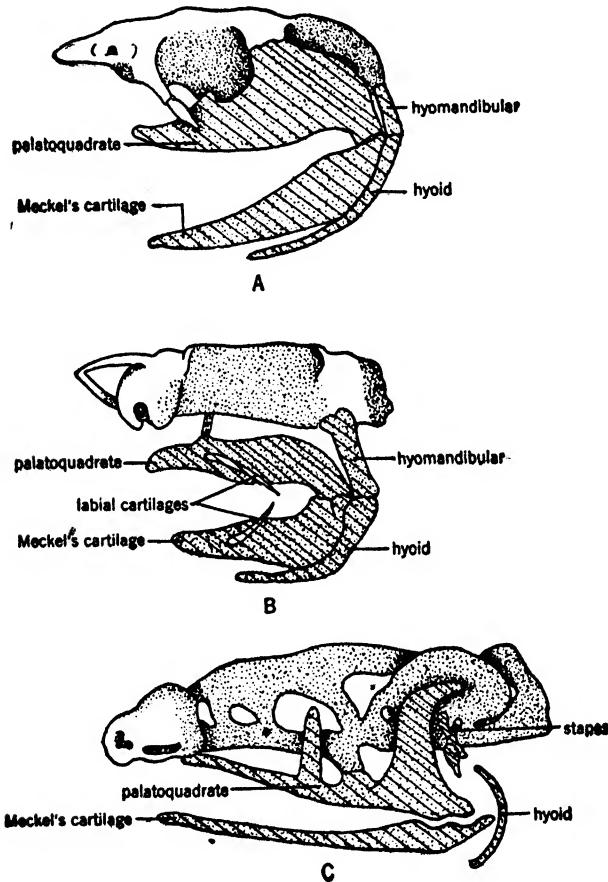
FIG. 93. Attachment of jaws to skull. A, amphistylic (primitive shark); B, hyostylic (Squalus acanthias); C, autostylic (chondrocranium of a tetrapod). After Goodrich.

The autostylic (Fig. 93 *C*) attachment found in the higher forms has the palatoquadrate bar firmly attached to the skull, the hyoid arch taking no place in the suspension. The lower jaw and the palato-quadrate bar bear teeth in the sharks, and it is over this cartilaginous foundation that the dermal bones of the higher forms are to be deposited.

The jaw of *Amia* is covered with dermal plates: a large dentary, which sheathes the anterior end; and the articulare, angulare, and surangulare, which cover the posterior end. There are several ossifications of the Meckelian cartilage. The inner surface is covered by the coronoid and splenial. The mandible of *Cyprinis carpio* (Fig. 94 *A*) is well developed but toothless and is made up of the dentary, articulare, and a small angulare. The jaw of *Anarrhichthys* consists of but three bones, the dentary, articulare, and angulare, and has large teeth for crushing
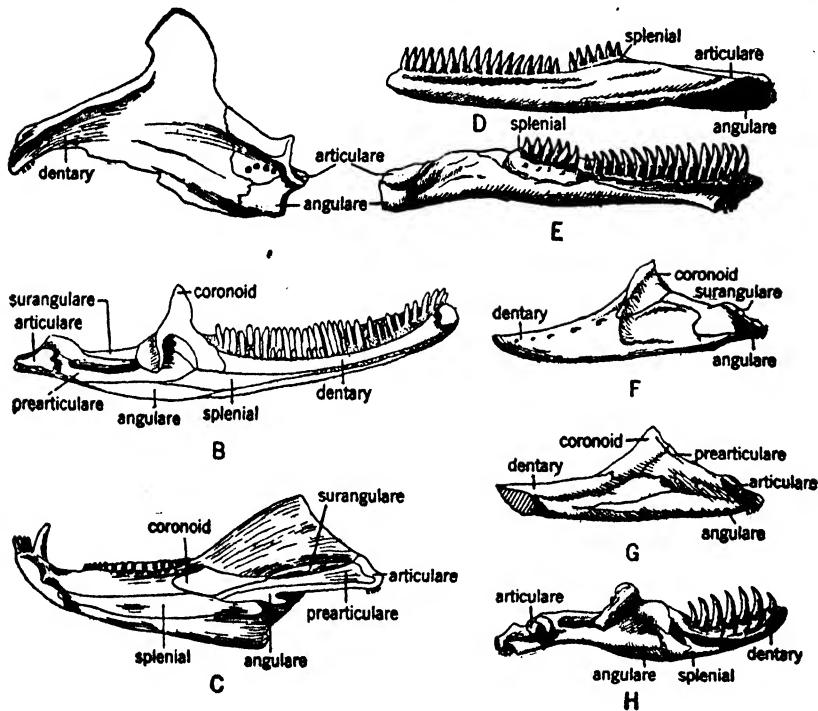
FIG. 94. Mandibles of different vertebrates to show their structure and elements. A, left mandible of carp (Cyprinis carpio); B, mandible of Sceloporus undulatus, inner face of left; C, inner face of mandible of cynodont lizard (after Broom); D, outer face of left mandible of Necturus; E, inner face of mandible of Necturus; F, outer face, and G, inner face, of mandible of turtle (Amyda spinifera); H, mandible of Heloderma, left, inner face.

The jaw of the early amphibians has a large number of elements inherited from fish ancestors. The jaw of the frog is quite simple, having an ossification of the Meckelian cartilage at the anterior end, the mento-Meckelian bone. *Necturus* is simpler than the frog, with a dentary, a toothed splenial, a cartilaginous articulare, and an angulare (Fig. 94 *D*, *E*).

The jaw elements of the reptiles generally are more numerous than in modern amphibians. *Heloderma* is typical, with a dentary, splenial, angulare, surangulare, and coronoid (Fig. 94 *H*). The ankylosis at the symphysis depends on the use, snakes (Fig. 95 *A, B*) generally retaining a loose symphysis, whereas in others it is ankylosed. (See Figs. 94 *B, C, F, G*.)

The therapsid jaw is quite significant, since it is used to explain the origin of the ossicles of the ear in the mammals (Fig. 94 *C*). The dentary is large, but the posterior elements are greatly reduced in size. There is an indication of a new articulation between the posterior end of the dentary and the squamosal.
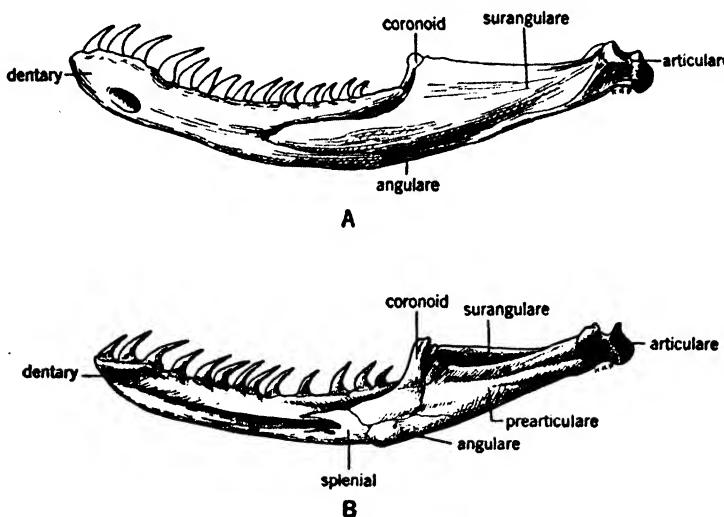
FIG. 95. Mandible of python. A, outer; B, inner face.

In birds the mandible (Fig. 306) is sheathed in a horny covering, and the individual bones are generally fused. Normally, the dentary, angulare, surangulare, and splenial are present, with traces of the coronoid in the embryo. Teeth of the early birds are typically reptilian in shape and structure. (Fig. 62.)

The mammalian jaw consists only of the dentary, since the other elements have been lost or shifted (Fig. 96 *A, B*). The jaws vary greatly, being light where little is required, and heavy where the need is evident. The condyles are variable according to the movement of the jaws, which may be in a straight vertical plane, or rolling as in the ungulates, or with an anterior sliding movement. Two foramina generally mark the mandible, the mandibular foramen at the base of

the coronoid process and the mental foramen (Fig. 96 *A*, *B*) on the outer face of the jaw in the chin region.

The visceral skeleton is a development associated with gills and their external openings, the gill slits, which had to be opened and closed in the work of respiration. The original reinforcing structure for the attachment of muscles was a series of bars or arches, varying in number from seven to nine, and possibly even more in ancient forms. In the sharks of the present day, each arch consists of several pieces of cartilage joined to a basal bar (Fig. 264). The dorsal piece, the pharyngo-branchial, is followed by an epi-, cerato-, and hypobranchial, with a
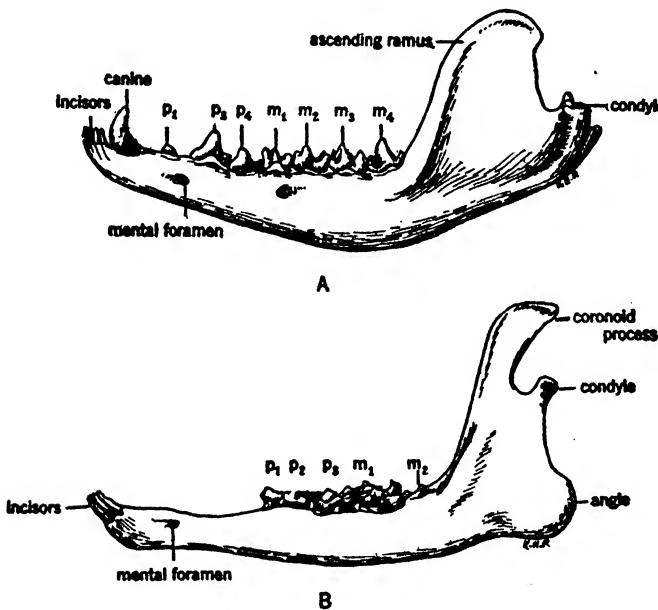
FIG. 96. Mammalian mandibles. A, opossum; B, deer.

basibranchial extending along the ventral bases. The labial cartilages of the shark possibly represent extra gill cartilages. The jaws of the shark and their supports are derived from the two anterior gill arches, the first forming the mandibular arch and the second the hyomandibular; the remaining arches support the gills. In tetrapods, these arches are utilized for other purposes or eliminated. The visceral arches of *Amia* are slightly but not completely ossified, the mandibular and hyomandib-ular regions being covered with bony plates after the manner of the higher teleosts. In teleosts all the parts of the visceral arches are ossified, and in some groups very interesting modifications are associated

with food habits, as in the carp where the last pharyngeals bear peculiar tooth-like structures.

The visceral skeleton of the Amphibia (Fig. 97 A) is still somewhat fish-like, especially in the urodeles, but is more specialized in the Anura. The visceral skeleton of *Necturus* consists of the hyoid series, with three epibranchials and traces of the fourth. This structure is necessary in *Necturus* because of the permanent retention of gills. In *Rana*
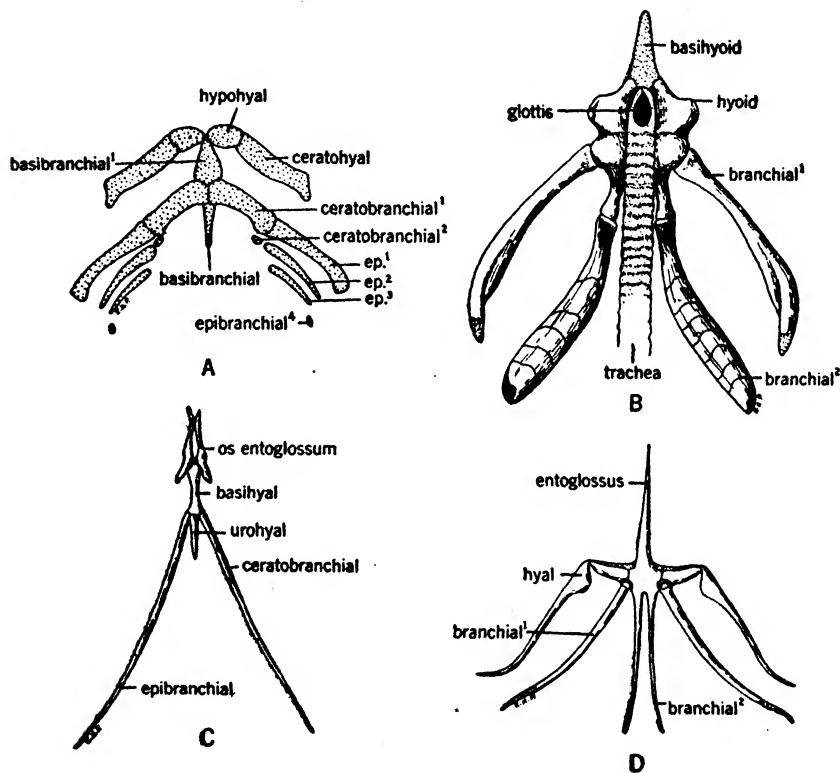
FIG. 97. Hyoid structures. A, Necturus; B, Amyda spinifera; C, Bird (Sialia s. sialis); D, lizard (Holbrookii maculata).

catesbiana, the visceral skeleton is an irregular piece, with parts much consolidated. The young tadpole has four epibranchials but loses them during metamorphosis.

Recent work by Noble has shown that, by means of endocrine gland extracts, certain changes can be initiated in forms that do not metamorphose normally, and that there is an attempt on the part of the visceral skeleton to approach the adult condition.

Since there is no metamorphosis in the reptiles, the visceral arches

are still more simplified. 'With better development of the lungs, the supports for its accessory structures are derived from the visceral arch material. The Chelonia (Fig. 97 *B*) have a bony basal plate and two epibranchials. *Chelydra serpentina* has a narrow basilingual plate, and the hyoid arch is reduced to a small bit of cartilage extending out laterally. The two pairs of cornua represent the first and second branchial arches joined by the basilingual plate. In *Ophidia* the
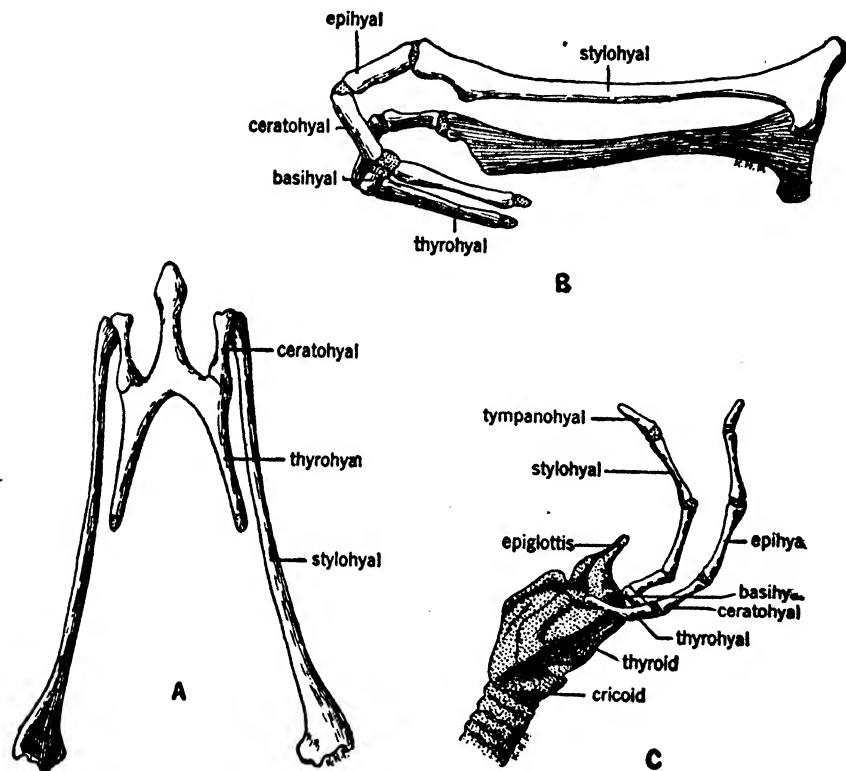
FIG. 98. Hyoid structures of mammals. A, horse; B, deer; C, after Jayne, lateral of cat.

hyobranchial apparatus is reduced to a pair of rods, the remains of the hyoids, lying along the trachea. (See Fig. 97 *B, D*.)

The hyoid apparatus of the bird (Fig. 97 *C*) is more simplified than in the reptiles, usually consisting of a processus entoglossus (or tongue process), a basihyal, a urohyal (or basibranchial), and a pair of horns (or cornua), consisting of a cerato- and epibranchial.

The hyoid arch of the mammal is quite variable within the class, since it is complete in some forms and much reduced in others. When

COMPARATIVE TABLE OF THE BONES OF THE SKULL IN REPRESENTATIVES OF THE FIVE CLASSES OF VERTEBRATES

CRANIAL ELEMENTS

Regions	Names of bones	*Cyprinis*	*Rana*	*Varanus*	*Gallus*	*Homo*	Remarks
Nasal	*Lateral ethmoid*			+			The vomer of mammals is a new bone.
	Nasal	+	+	+	+	+	
	Mesethmoid*			+			
	Vomer	+	+	+	+	+	
	Septomaxillary			+			
	Preethmoid	+					
Frontal	**Frontal**	+	+	+	+	+	Joined to the parietal in *Rana*.
	Prefrontal	+		+			
	Postfrontal	+					
	Lacrimal	+		+	+	+	
	Supraorbitals (v)	+		+			
	Suborbitals (v)	+					
	Postorbitals			+			
	Sclerotics	+	+	+	+		
	Orbitosphenoid	+		+	+	+	} These four are usually joined in mammals to form one bone, the sphenoid.
	Presphenoid*					+	
Parietal †	*Alisphenoid*	+			+	+	
	Basisphenoid*			+	+	+	
	Parietal	+	+	+	+	+	Joined to the frontal in *Rana*
	Sphenotic	+					
	Pterotic	+					
Ear	*Epiotic*	+				+	} These three are joined in mammals to form the petrous portion of the temporal.
	Prootic	+	+	+	+	+	
	Opisthotic					+	
	Squamosal	+	+	+	+	+	
	Tympanic					+	In embryo only, from reptilian angulare.
Occipital	*Supraoccipital**	+		+	+	+	Often has a dermal element added.
	Exoccipital	+	+	+	+	+	
	Basioccipital*	+		+	+	+	
Palatal	**Palatine**	+	+	+	+	(pal.)	} A process on the palatine in man. pt. = pterygoid. tr. = transpalatine. al. = alisphenoid. vo. = vomer.
	Endopterygoid	+	pt.	pt.	pt.		
	Ectopterygoid	+	tr.	tr.			
	Metapterygoid	+					
	Epipterygoid			+		al.	
	Parasphenoid*	+	+	+	+	vo.	
Upper jaw	**Premaxilla**	+	+	+	+	+	} Fused in man.
	Maxilla	+	+	+	+	+	
	Jugal	+	+	+	+	+	
	Quadratojugal		+	+	+		
	Quadrate	+	+	+	+	in.	in. = incus.
Lower jaw	**Dentary**	+	+	+	+	man.	man. = mandible.
	Coronoid			+	+		
	Splenial		+	+	+		
	Angulare	+	+	+	+	ty.	ty. = tympanic.
	Surangulare			+	+		
	Articulare	+	+	+	+	mal.	mal. = malleus.

VISCERAL ELEMENTS

Regions	Names of bones	*Cyprinis*	*Rana*	*Varanus*	*Gallus*	*Homo*	Remarks
Hyoid arch	*Hyomandibular*	+	st.	st.	st.	st.	st. = stapes. col. = columella.
	Symplectic	+	col.	col.	col.		
	Interhyal	+					
	Epihyal	+					} These five become the hyoid series of tetrapods.
	Ceratohyal	+					
	Hypohyal	+					
	Basihyal*	+					
Gill covering	**Preopercular**	+					
	Opercular	+					
	Subopercular	+					
	Interopercular	+					

Membrane bones in bold-face type.   Cartilage bones in italics.
* Median, single elements are marked by asterisk.   (v) Variable in number.
† The dermal interparietal usually joins the supraoccipital.   (See Figs. 85, 86.)

complete, it consists of a tympanohyal, stylohyal, epihyal, ceratohyal, and basihyal. The uses of the structure are limited to the support of the tongue, and the building of the larynx, trachea, and parts of the ear. (Figs. 98 *A*, *B*, *C*, 187, 188, 189.)

Vertebral Column

The notochord appears suddenly in the geological history of animals, with no definite forerunner that has so far been discovered. The chordates were represented in the Cambrian period by ostracoderms with their peculiar adaptations, and although their notochord is not known, we may safely assume that it was present. In *Amphioxus* the notochord has a definite chordate condition, and here it is a somewhat elastic rod extending from the tip of the tail to the tip of the nose (Fig. 1). It ends near the otic capsule in sharks. Its develop-
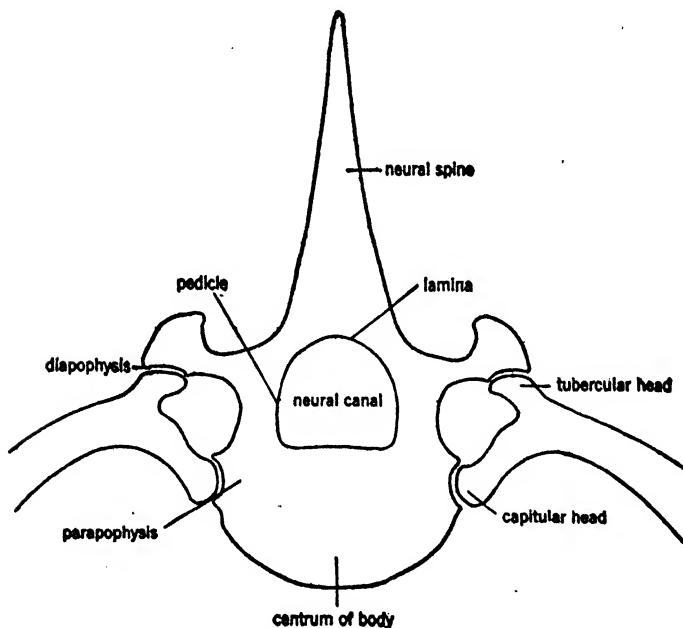
Fig. 99. Diagram of a typical thoracic vertebra.

ment appears to be from the endoderm, and though its form and even its origin may vary, it has a characteristic appearance in all vertebrates and is one of the landmarks of embryological sections, since it is usually vacuolated, and unlike any other structure. Typically the notochord is covered by an inner sheath (elastica interna) and an outer sheath

(elastica externa), both of which may be concerned in the formation of
the vertebral column.

The unit of the vertebral column is a vertebra, which is the end
product of a long series of developments from a condition in which
nothing but the notochord is present to the completed vertebra with
its specializations. Typically, a vertebra (Fig. 99) consists of a body,
or centrum, which is formed around the notochord. It is usually
heavy, since the vertebrae must articulate with one another, and there
must be some means of making this articulation strong yet flexible.
Various devices have been used for this purpose. The centra them-
selves have been modified at the ends to assist in joining of the vertebral
units. (See Fig. 101.) Acoelous vertebrae are flat at both ends of the
centrum; procoelous are those in which the anterior end of the centrum
is concave; opisthocoelous, those in which the posterior end of the
centrum is concave; amphicoelous, in which both ends of the centrum
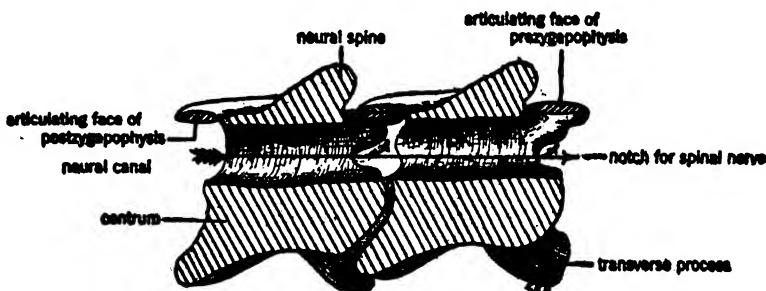
Fig. 100.   Sagittal section of two articulated vertebrae.

are concave (Fig. 101). Some vertebrae have both ends of the centrum
with distinct convex knobs. Pads of cartilage are interposed between
the vertebrae. Dorsal to the centrum, the neural canal for the passage
of the spinal cord is roofed over by the lamina, with pedicles forming the
sides. A neural spine may be present for the insertion of muscles. Tail
vertebrae of many vertebrates have a ventral, haemal process, which
forms an arch for the blood vessels extending to the tail, and may have
a haemal spine. The articulation is further strengthened by the de-
velopment of special processes, the pre- and postzygapophyses, which
form an interlocking yet flexible link between two vertebrae. A pair of
prezygapophyses are developed on the neural arch with their articular
faces pointing dorsally; the postzygapophyses are developed at the
posterior end of the vertebra with their articular faces pointing ventrally.
The postzygapophyses of one vertebra rest on the articulating face of
the prezygapophyses of the vertebra posterior to it (Fig. 100).

Snakes and some reptiles develop a third pair of processes, a zygantrum and a zygosphene, the zygantrum being on the posterior region of the neural arch, with the reciprocal structure, the zygosphene, on the anterior region of the neural arch. These seem to be necessary because of the demand for strength, especially in the pliable column of the snakes. The thoracic vertebrae have large processes on the neural arches and centra for the articulation of the ribs. A dorsal diapophysis supplies the articulation for the tubercular head of the rib, and the ventral parapophysis supplies the articulation for the capitular head. Lumbar vertebrae have these processes fused to form · a transverse process, giving them a characteristic form. Cervical vertebrae may have a median ventral ridge on the centrum, the hypapophysis.

The cyclostomes present important features in the development of the vertebral column. The notochord persists as the main element in the axial skeleton, and in the myocommata dorsal cartilaginous riders develop that arch over the nerve cord, and corresponding ventral
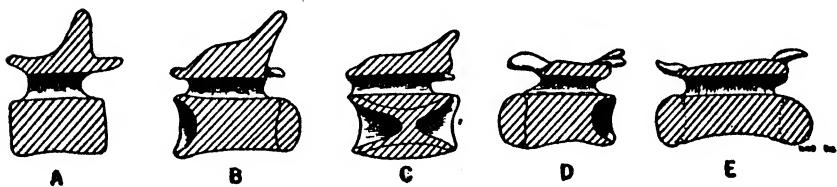
FIG. 101. Types of centra. A, acoelous; B, procoelous; C, amphicoelous; D, opisthocoelous; E, biconvex.

riders form haemal arches to protect the blood vessels. No centra are developed to unite these arches, and the notochord is not constricted in any way.

The sharks develop the vertebral column into a series of cartilaginous parts which may be calcified and hardened. Neural and haemal arches are developed with intercalaries. The centrum is formed in two ways, with characteristic effects on the notochord. The asterospondylous vertebrae are formed by invasions of cartilage into the tissue of the notochord, and the cyclospondylous vertebrae are formed by constrictions of the notochord, so that the finished centrum shows concentric rings. *Acipenser* and many of the fossil crossopterygians, such as *Caturus*, show the elements of the vertebrae clearly separated. These elements are joined together in the vertebrae of the teleosts, each vertebra being well formed with a centrum, a neural arch, and (in the tail) a haemal arch. Means of interlocking the vertebrae have also appeared and are present in the teleosts. Double centra are

found in the tail of *Amia*, where the anterior and posterior halves of the centrum do not unite — a condition known as diplospondyly.
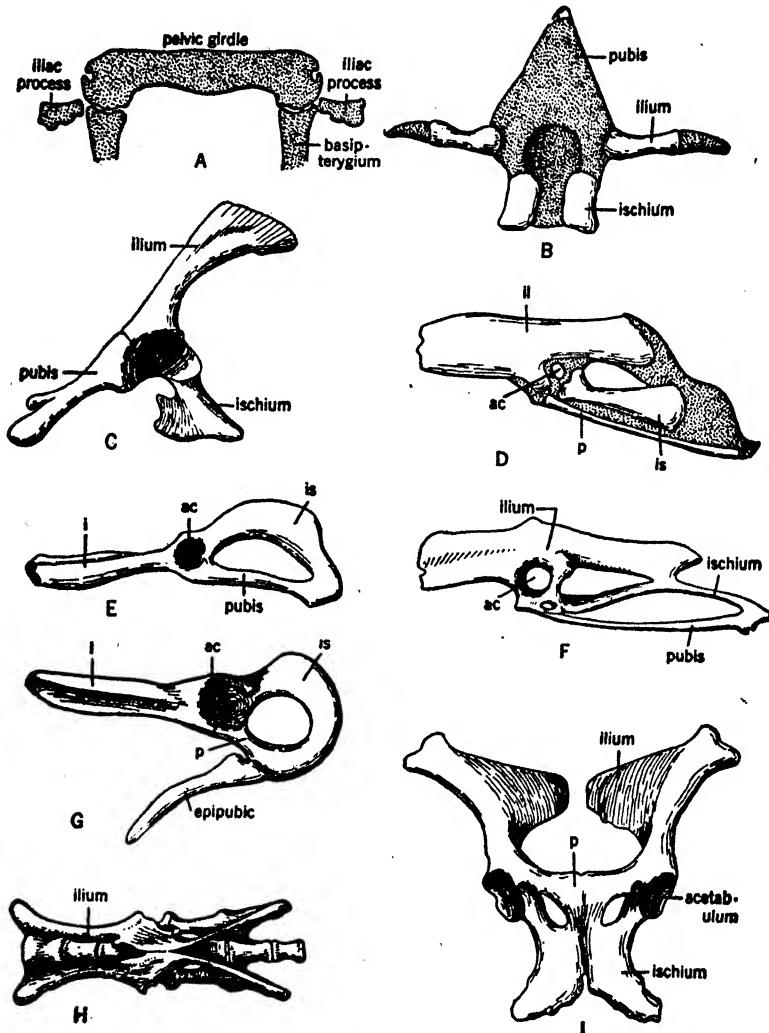
FIG. 102. Types of pelvic girdles. A, shark (Squalus); B, mud puppy (Necturus); C, turtle (Chelydra); D, chicken (Gallus); E, muskrat (Odonatra); F, rhea; G, opossum (Didelphis); H, mole (Scalops); I, horse (Equus).

The vertebrae of the amphibians are very varied, especially in the Stegocephalia. Structurally, each vertebra consists of eight pieces, four on each side: the basidorsalia, interdorsalia, basiventralia, and interventralia. By different combinations of these parts, various types

of vertebrae are formed. These parts develop from sclerotomes, each vertebra being formed from two, the anterior half of one and the posterior half of the sclerotome preceding (Fig. 3).

The vertebral column shows a progressive growth and development as the higher forms are approached. The teleosts have but two regions,
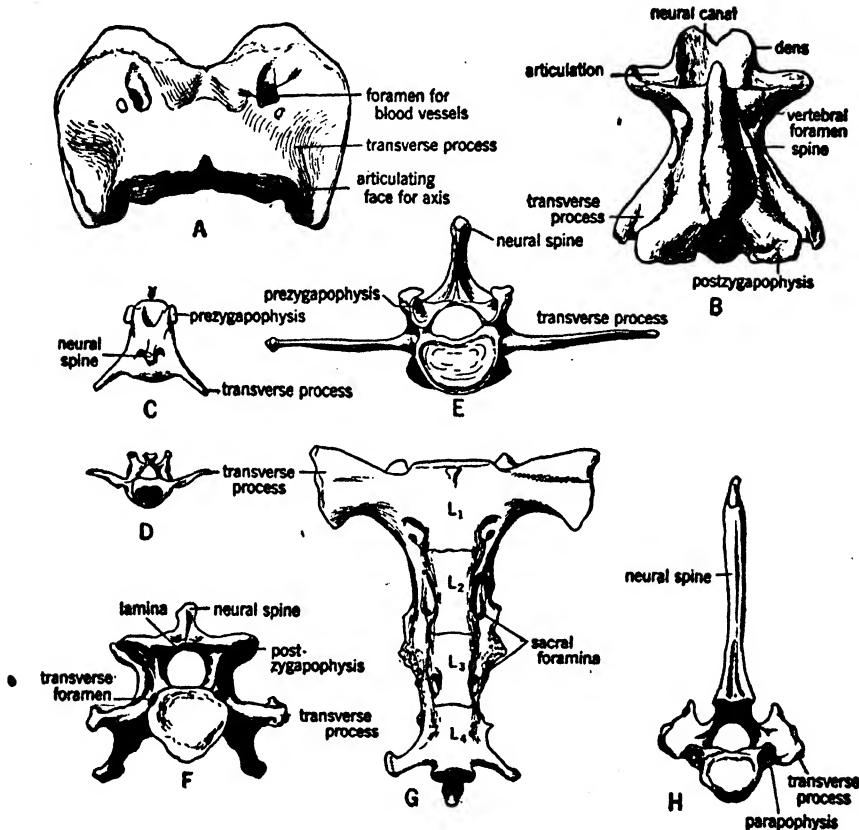
FIG. 103. Vertebra of a sheep from different regions of axial skeleton. A, atlas, dorsal face; B, axis (epistropheus) dorsal face; C, caudal, dorsal; D, caudal, posterior; E, lumbar, anterior; F, cervical, posterior; G, sacrum, ventral; H, thoracic, posterior.

the trunk and the tail, the caudal vertebrae differing in having haemal arches. The Amphibia have more differentiation, with the vertebral column divided into a cervical, trunk, sacral, and caudal region. The reptiles have five regions fairly well differentiated, with cervicals, thoracics, lumbars, sacrals, and caudals. The cervicals, however, still retain ribs, the thoracics are modified for rib articulations, and the

lumbars are freeing themselves of ribs to gain more freedom of action. The sacrals are acquiring better articulations for the pelvic bones, and though the number is still small (two or more), the typical sacrum is being approached in form. The dinosaurs, with a bipedal gait and hopping legs, developed a sacral region resembling that of the birds and probably for the same reason. The pterodactyls paralleled the birds in joining a number of the vertebrae to form a sacrum. Snakes develop
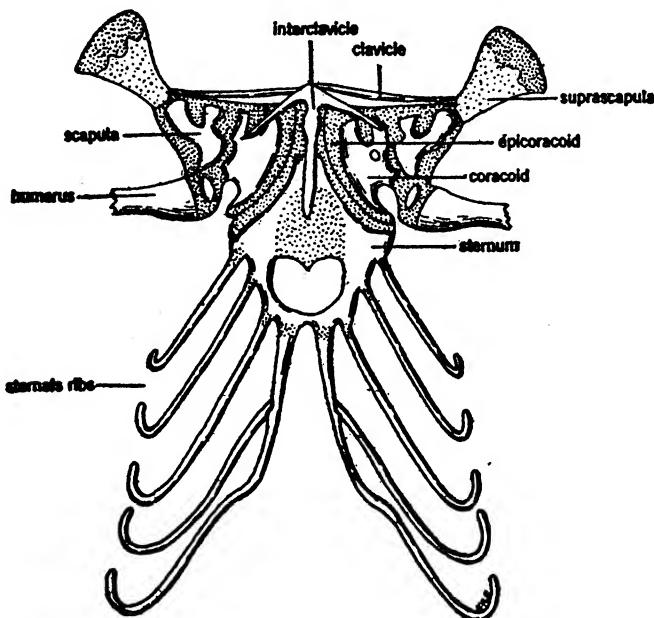
FIG. 104. Sternum and shoulder girdle of lizard, Holbrookii.

a very motile skeleton in which there is great freedom of motion yet the strongest union of the individual vertebrae by extra processes, the zygantra and zygosphenes.

The modern bird has a highly specialized vertebral column, since a rigid body is required for flying. The vertebrae have peculiar saddle-shaped centra found in no other class. The ribs of the flexible neck are shortened and ankylosed to the vertebrae. The thoracic vertebrae are joined to form a notarium. The synsacrum includes a part of the thoracics, lumbars, sacrals, and some of the caudals.

The vertebral column reaches its highest development in the mammals. The number of vertebrae in each region is fairly definite except in the edentates.

The cervical region in mammals consists of ring-like vertebrae, which

give great pliability and strength.   The first two vertebrae, the atlas and axis (Fig. 103 *A*, *B*) are very characteristic, the atlas being broad with no centrum, and the axis (or epistropheus) having an odontoid process derived from the centrum of the atlas.   The other cervicals (Fig. 103 *F*) have vestigial ribs that are ankylosed to the centra, the ribs being reduced to small processes forming the passageway for the vertebral artery.   With pre- and postzygapophyses, greater flexibility is obtained.   The skull gets its movement by action between the atlas and the axis, and by the twist of the whole cervical series.   The centra are acoelous in the mammals, with few exceptions.   Those of the cervical region in ungulates are opisthocoelous.

The thoracic vertebrae (Fig. 103 *H*) in mammals are characterized by strong neural spines, small centra, and facets for the articulation of the ribs.

The lumbars (Fig. 103 *E*) have no articulating processes for ribs, the spines being inclined anteriorly, and conspicuous transverse processes extend out laterally from the centra.   The centra widen out at the

THE NUMBER AND DISTRIBUTION OF THE VERTEBRAE IN SOME VERTEBRATES

	Cervicals	Thoracics	Lumbars	Sacrals	Caudals	Total
Man............	7	12	5	5	3–4	32–33
Cat.............	7	13	7	3	18–25	48–53
Bradypus (three-toed sloth)	9	(thoracics + lumbars) 20		6	11	36
Opossum........	7	13	6	2	19–35	47–63
Gallus...........	16	5	8	2	9+ pygostyle	40+ pygostyle
(Synsacrum consists of 1 thoracic, 8 lumbars, 2 sacrals, 4 caudals)						
Alligator........	8	11	5	2	40+	67+
Python..........	(Regions not clearly differentiated)					435
Necturus........	1	(thoracics+lumbars) 18		1	23+	43+
Cyprinis........		(Body) 17			17	34

posterior end of the series to meet those of the sacrum. Some interesting devices are developed in the lumbar region of the ungulates, particularly in the artiodactyls, where the pre- and postzygapophyses are so shaped as to interlock and thus strengthen this region.
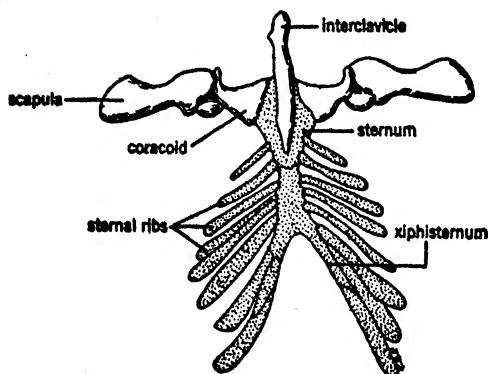
FIG. 105. Sternum and shoulder girdle of alligator.

The sacral region (Fig. 103 *G*) includes a number of vertebrae, varying from two to thirteen. There is a tendency for this series to coalesce in the adult to form a single piece, but the outlines of the individual vertebrae are usually definite, as shown by the suture lines. The sacrum varies greatly in shape, since it is very closely correlated with the activities of the animal and with the type of pelvis attached to it.

The vertebrae of the tail become modified toward the end, until nothing but the centrum remains. Except in mammals that make use of the tail as a prehensile organ, the development of pre- and postzygapophyses is weak. The neural arch is carried on the first part of the series but is gradually reduced and finally lost entirely. Haemal arches, or chevron bones, are found in some mammals such as monotremes, marsupials, and rodents.

Ribs

The haemal ribs present in fishes are subperitoneal structures possibly derived from haemal arches; the pleural ribs, also found in some fishes, as well as in higher animals, are formed in the myocommata between muscle segments. Both types are found in *Polypterus*. Originally extending along the whole length of the body, ribs become more and more restricted in the higher animals, until they are confined to the thoracic region in mammals. The ribs of fishes are attached low on the centra, and their ends are not connected on the midline, since no sternum is present. In the amphibians, they are a little more varied and are generally bicipital, having a capitular and a tubercular head, but are not connected with the sternum. In reptiles the sternum is well developed, and the ribs are attached to it for the first time, to form a complete thoracic basket. There is still a tendency, however, for the

ribs to extend the whole length of the body. Generally the ribs are bicipital in reptiles. Uncinate processes, joining adjacent ribs, are present in *Eryops*, alligators, and *Sphenodon*. The ribs of turtles become specialized and ankylosed together to help in forming the carapace. In birds the cervical ribs are ankylosed to the vertebrae and the thoracic ribs are joined by uncinate processes. The thoracic ribs (Fig. 99) of the mam-

FIG. 106. Sternum and shoulder girdle. A, eagle; B, pelican.

mals are articulated with the sternum except for a small number of floating ribs. They are bicipital and articulate with the centra, the capitular head with the parapophysis and the tubercular head with the diapophysis.

Sternum

With the development of the ribs, the circle of bone around the body was completed in the thoracic region except along the mid-ventral line. The development of the sternum in the tetrapods completed this gap.

FIG. 107. Sternum and shoulder girdle of duckbill (Ornithorhynchus).

The sternum not only supplies the support needed for the shoulder girdle but also provides an area for the insertion of some of the muscles of the fore limb. Its origin appears to be from the fused ends of the ribs. It is not found in the elongate, snake-like forms. In *Cryptobranchus* it is merely a heart-shaped cartilage, articulating with the two coracoids, but in *Rana* it reaches a higher development with a presternum, sternum, and xiphisternum. No ribs are attached to it in the amphibians. In reptiles (Fig. 105) there is a beginning connection between the ribs and the sternum. The lizard *Holbrookii* (Fig. 104) has four ribs attached, and the coracoids are well articulated. Birds have a striking sternum, since flying depends upon the large pectoral muscles,

and the sternum supplies the surface for their attachment (Fig.

FIG. 108. Sternum of rat.

106 *A*, *B*). In cranes and swans a part of the trachea is coiled within the sternum, showing the double origin of this now single structure. The bracing in birds is perfect, because of the articulation of the coracoids and the close connection with the clavicles. The sternum of mammals is somewhat simplified except in the monotremes (Fig. 107), where the reptilian appearance remains. In mammalia (Fig. 108), a number of sternalia are developed, as in the rat, where there are a presternum, six sternalia, and a xiphisternum.
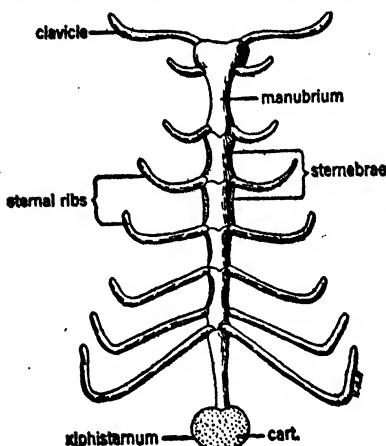
Episternum (interclavicle)

The episternum (Figs. 104, 105) is a small median element applied to the ventral side of the sternum. It is found in amphibians and reptiles but is not represented in mammals, unless the median element of *Ornithorhynchus* is homologous. It is well developed in the Lacertilia, Crocodilia, and other reptilian forms.

Splint-like dermal bones known as abdominal ribs (Fig. 109) or gastralia were developed in the stegocephalians and are present as conspicuous skeletal parts in Crocodilia, *Sphenodon*, and other reptiles. They were also present in *Archæopteryx*, the earliest bird. They cover the

FIG. 109. Gastralia or abdominal ribs of alligator.

region between the sternum and pelvis, to protect the soft parts not protected by ribs.

APPENDICULAR SKELETON

Three theories have been suggested for the origin of fins: the gill arch theory of Gegenbaur, the fin-fold theory advanced by Thacher and elaborated by several European writers; and the external gill theory of Kerr. Gegenbaur and his followers assumed that gill arches slipped along the body and developed into the pectoral and pelvic girdles and fins. Little evidence has been found to support this assumption, and few fossil or modern fishes have the type of fins that would result from such an origin. The fins themselves, after this theory, would have come from the branchial rays, thus having a median axis with small pieces of material along the sides, somewhat similar to those of *Neoceratodus*.

The fin-fold theory (Fig. 110) has more support in the way of positive evidence, although it is not all conclusive. According to Thacher,
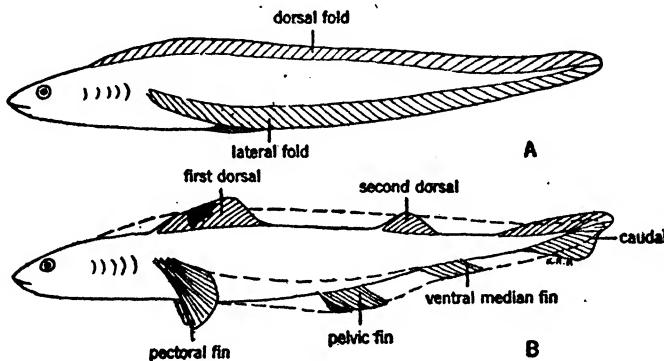
FIG. 110. Diagrams illustrating the fin-fold theory of the origin of fins. A, continuous folds; B, folds broken up into regions. After Wiedersheim.

the appendicular skeleton developed in two pairs of primitive folds running along the sides of the body. The more dorsal pair of folds approached the dorsal line and finally formed a median fold extending the entire length of the body and around the tail to the vent. The ventral pair of folds extended from the head region along the side walls to the vent. These folds were gradually supported by the ingrowth of mesoderm, and finally became fin-like in their basic structure. These folds assisted in keeping the balance and in preventing a corkscrew motion while the animal was moving through the water. It is assumed that the lateral folds were capable of movement at two regions along the sides, and that these two centers of action were eventually separated, becoming the anterior and posterior pairs of fins. The lappet-like appendages of the placoderms, *Cladoselache*, and early elasmobranchs seems to be in line with this theory. A third theory,

that of J. Graham Kerr, comes from an embryological study of primitive fishes and dipnoans. It is a modification of the gill arch theory of Gegenbaur, in that the limb girdles are derived from visceral arches, but differs, by deriving the fins and limbs from external gills. The external gills occur in the embryological development of primitive fishes and amphibians. Besides respiratory functions, these external gills may serve as balancers, since they are supplied with a musculature and are capable of movement.

The median fins may be built up entirely of connective tissue and skin, or they may have supports of different kinds. Placoderms had spines and curious elements along the median line of the back which may be interpreted as median appendages. The elasmobranchs have cartilaginous supports consisting of basalia, which come in contact with vertebrae, and a radial series in the fin itself. Long feathery supports in the fin may be horny, as in the sharks, dipnoans, crossopterygians, and teleosts. Median folds or fins appear in young amphibians and in all urodeles that remain permanently in the water. The median fins that develop in ichthyosaurs, and those found in water mammals such as whales and dolphins, consist of adipose tissue and are practically without supporting structures.

FIG. 111. Left shoulder girdle of teleost (Ictiobus).

Paired appendages appeared early in vertebrates and are practically universal in the subphylum. *Cladoselache* had pairs of lappet-like fins with broad bases but not yet connected with internal girdles. The higher elasmobranchs developed a pectoral girdle in the form of a U-shaped piece of cartilage connecting the anterior fin. Elements were added in higher fishes to tie the pectoral girdle to the skull. These elements, consisting of the cleithrum and several small supracleithra (Fig. 111), are of dermal origin. The scapula and coracoids, developments from the cartilaginous skeleton, which lie along the inner side of the cleithrum, supply an articulation for the fin. The origin of the clavicle is not clear, and in the higher forms it probably consists of both dermal and chondral elements. The interclavicle (Figs. 104, 105), which first appears in the stegocephalians, persists in reptiles, birds, and monotremes. There are two bracing elements in the amphibians, the coracoid and the procoracoid. Reptiles add a third, the epicoracoid. Monotremes retain both the procoracoid and the coracoid, but

other mammals do not have these as separate elements, retaining only the posterior element which is attached to the scapula as the coracoid process.
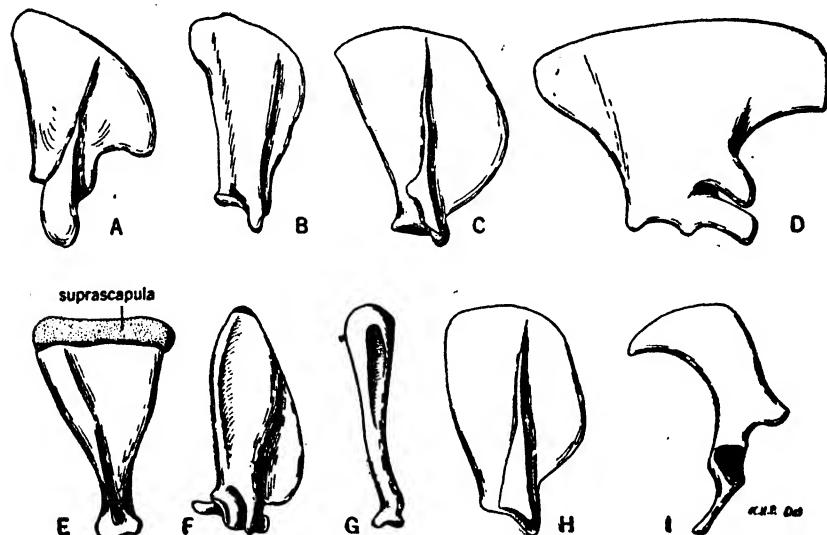
FIG. 112. Scapulae of mammals. A, gorilla; B, monkey; C, mountain lion; D, dolphin; E, deer; F, bat; G, mole; H, opossum; I, duckbill (monotreme).

Anterior Girdle

The anterior girdle of the shark (Fig. 270 A) consists of a U-shaped band of cartilage that extends around the body on the ventral side. In the young there is a differentiation into parts, but in the adult these fuse into one mass. The crossopterygians add a series of dermal elements, the first of which is connected to the skull. The cartilaginous band, though still large in *Acipenser*, is much reduced in *Amia*, where the cleithrum is enlarged to support the scapular elements, and a series of smaller dermal plates connect this cleithrum with the skull. The clavicles, a pair of ventral elements, are found in the older groups of fishes (*Polypterus* and fossil crossopterygians), but in teleosts they are replaced by the large bony cleithra, which meet on the mid-ventral line. A modern teleost has very large cleithra (Fig. 111), which are articulated to the skull through several small elements and are braced by a pair of long, thin postcleithra or postclavicles. The cartilaginous band has ossified into three pairs of elements in *Cyprinis*, a scapular, mesocoracoid, and coracoid.

The stegocephalians retained several fish-like structures, among

them the large cleithrum. *Cacops*, an early form, had a girdle consisting of a clavicle, interclavicle, cleithrum, and two coracoids. Probably there was a large cartilaginous mass representing the chondral elements. Modern amphibians have a much simpler girdle, *Necturus* having a suprascapula, scapula, procoracoid, and coracoid. The frog has a well-organized girdle, consisting of a suprascapula, scapula, procoracoid process, coracoid, and median epicoracoid cartilage.

Fig. 113. Girdles and fins of Cladoselache. A, anterior fin and girdle; B, posterior fin and girdle. After Jaekel.

The early reptiles, such as *Diadectes*, had a girdle much like that of the Stegocephalia, but in modern reptiles (Fig. 104) there is a complete reorganization. The connection with the sternum is improved, and there is a firm bracing by a clavicle and, generally, a coracoid and epicoracoid. The scapula and suprascapula complete the girdle. The alligator (Fig. 105) simplifies the girdle until it consists of only three elements — suprascapula, scapula, and coracoid.

The modifications necessary for flight develop in carinate birds, and their girdle is firmly braced by the scapula, coracoid, and furcula or clavicle (clavicle + interclavicle). The ratites lose the clavicle, and their girdle is much reduced and has a flat sternum lacking the keel.

The mammalian girdle is much reduced except in the monotremes, which retain the reptilian type. In *Ornithorhynchus* (Fig. 107) a large interclavicle, or episternum, forms the connection with the sternum, the coracoid is attached to the scapula, a small procoracoid is present,
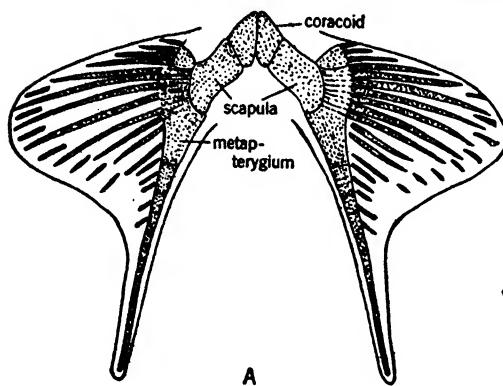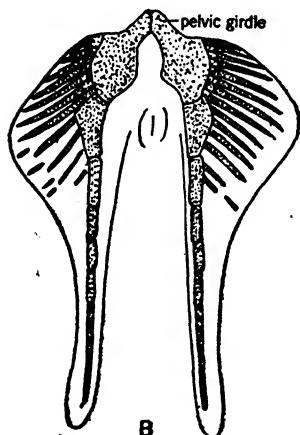
and a clavicle completes the girdle. Marsupials and placentals retain nothing but the scapula and clavicle, the scapula having a coracoid process which is separate in development. (This is considered by Romer as the procoracoid.) The clavicle (Fig. 108) is an element useful in climbing, and it is retained in animals that climb or have an arboreal ancestry. It is also found in embryos of ungulates. The tying of the scapula to the sternum is very important in any animal that is able to hold its weight by its anterior limbs. The scapula consists of a flat
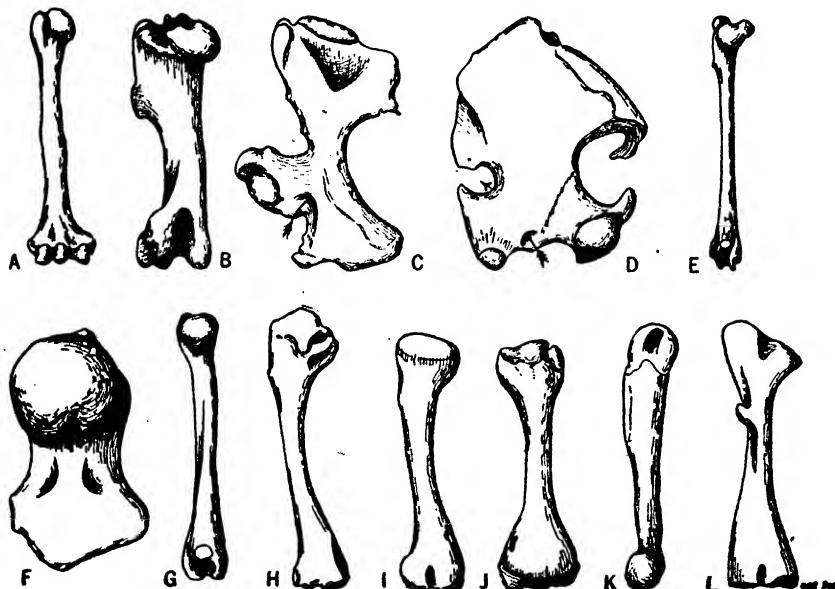
FIG. 114. A series of humeri (left) drawn to the same size to show variations in the different vertebrate classes. A, gorilla; B, horse; C, spiny anteater (Echidna); D, mole (Scalops); E, rabbit (Lepus); F, dolphin; G, cat; H, chicken (Gallus); I, alligator; J, Gila Monster (Heloderma); K, frog (Rana); L, salamander (Ambystoma).

blade, generally with a spine, and has an acromion process and a coracoid process. A cartilaginous suprascapula (Fig. 112 E) lengthens the blade on its dorsal border. The scapulae of the different groups are quite characteristic, and it is evident that their shape depends on the work that they do. Scapulae may be long and have a small spine, as in the ungulates; extremely elongated, as in insectivores; rounded, as in the carnivores; or rounded and flat with no spine, as in the dolphins. A long acromion process is generally associated with climbing (Fig. 112).
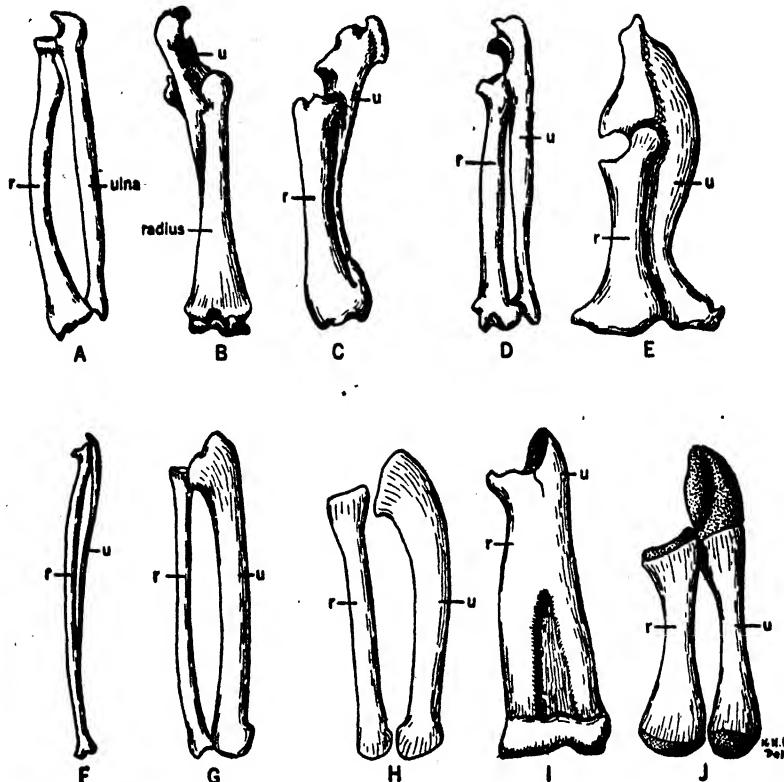
Fig. 115. Series of bones of the forearm to show variations of radius and ulna in different vertebrate classes. A, ape (Orang); B, horse (Equus); C, cow (Bos); D, cat (Felis); E, mole (Scalops); F, bat (Pteropus); G, turkey (Maleagris); H, alligator; I, frog (Rana); J, mud puppy (Necturus).

Posterior Girdle

The pelvis, or posterior girdle, serves two main functions: first, to supply a solid articulation for the femur; and second, to supply insertions and origins for the many muscles connected with the posterior limbs. It differs from the pectoral girdle in that it is always deep in the tissues and has never had any additions from dermal sources. Above the fishes, it is always attached to the vertebral column, lightly in the Amphibia, with a gradual improvement of the articulation through to the mammals. Each half consists of three elements, the ilium, pubis, and ischium. The ilium, or dorsal element, which always articulates with the sacrum, is variable in shape, depending on the type of work required of it. It is usually a straight bar but is T-shaped in birds and

ornithischian dinosaurs. The pubis, or ventral element, extends anteriorly except in birds, and it may join its fellow of the other side tó form a ventral arch. The obturator nerve generally extends through a large foramen in the pubis. The distal ends of the pubis and ischium may be joined, as in some of the birds and reptiles. Monotremes and marsupials have the epipubics, which hold up the marsupial pouch. The ischium, or posterior ventral element, is generally large, and it may join its fellow of the other side to form an arch. The acetabulum, or the socket, with which the head of the femur articulates, is formed by the bones of the pelvic girdle. Sometimes an acetabular bone is formed as a separate ossification.

The origin of the pelvic girdle is suggested in the elasmobranchs by a bar of cartilage (Fig. 102 A) between the fins that seems to have been a part of the fin-base. Crossopterygia develop two bony bars and the teleosts have the same type of structure, which seems to be a part of the fin-base extending into the body wall. Definite pelvic structures first appear in the amphibians, and they may be correlated strictly with tetrapods and land life. The connection between the ilium and the vertebral column is made first in the amphibians. It appears to be a new articulation in *Necturus* (Fig. 102 B), for it is very variable, and its position on the column may shift forward or backward. Each half of the girdle of *Necturus* consists of an ilium, an ischium, and a large

Fig. 116. Diagram showing the right hand of perissodactyl (A), and artiodactyl (B). A, mesaxonic; B, paraxonic. After Weber.

ventral cartilage from which the pubis may ossify. Much of the girdle remains cartilage in the urodeles. The high specialization found in the Anura is, of course, correlated with the jumping habits of this group. The reptiles (Fig. 102 C) show much variation of the pelvis, owing to different walking adaptations. Generally the girdle is very solid and substantial, its structure showing close correlation with the needs of land life. The attachment to the vertebral column is through one or more specialized sacral vertebrae, generally two in number in modern forms, but in the highly specialized reptiles such as *Trachodon* there were eight or nine. The pelvis is always triradiate (Fig. 102 C) and

generally has a large opening between the pubis and the ischium. Usually all three bones take a part in forming the acetabulum, the socket which supplies the articulation for the head of the femur.

In birds the pelvis is also a highly specialized structure, adapted to bipedal habits (Fig. 102 *D*, *F*). The ilium is greatly elongated and attached to the synsacrum. Except in the ratites, there is no fusion between the two sides. The pubics of adults are directed posteriorly — a secondary condition, since in the embryo they are as those of the reptiles.

In mammals the three elements of the posterior girdle tend to fuse into one piece, so that the separate bones are not distinct, but the triradiate structure is retained. The shape of the ilium varies with the habits; it is generally long in running animals; wide and extending out laterally in heavy, peg-legged animals, such as the rhinoceros and the elephant; rounded in apes and man; and vestigial in whales and sea-cows. The epipubics (Fig. 102 *G*) found in the monotremes and marsupials, are sometimes present in the embryos of placentals. In man the pelvis is called the innominate bone (Fig. 102).

Fins

The median fins of the fishes consist of various modifications of the original median fin-fold, which was at first continuous and without skeletal supports. Early in the history of the fishes these supports developed and formed the basis for median fins. In cartilaginous fishes the radial distal elements, or axinosts, extend into the fin and are in contact with the horny rays; the basal proximal elements, or baseosts, are in contact with the vertebral column. In teleosts the skeletal part of the median fin becomes more complex (Fig. 267), bony rays being developed that make a much better contact with the skeleton. The neural spines are grooved on the anterior side to form an articulation with the radio-basals and thus build up a good mechanical structure in combination with the dermal supports.

The tail fin, which is the main propelling device in most water animals, was originally a part of the median fold which extended around the body, as in the cyclostomes. Primitively, it was without supports and therefore of little use as a propeller. The shape was rounded or pointed, at first, with the blades equal and the axis in the middle. This diphycercal tail (Fig. 263) is found in cyclostomes, dipnoans, crossopterygians, primitive sharks, and many deep-sea teleosts. The heterocercal type (Fig. 263), found in modern sharks, sturgeons, paddlefish, and other forms, is two-lobed with the main axis extending

into the dorsal lobe (Fig. 269), while the ventral lobe is smaller and formed by fleshy tissue. The homocercal tail (Fig. 263), found in most teleosts, is a modified heterocercal type in which the lower lobe is developed so that it is equal to the dorsal, thus forming a symmetrical structure, but the axis still extends into the dorsal lobe (Fig. 269). The gephyrocercal tail (Fig. 263) is really a modified heterocercal in which the tail appears to be symmetrical, but retains the asymmetrical supporting structures.

Paired Appendages

There appears to be no doubt that the tetrapod limbs have been derived from fins, though the mode of transformation is uncertain. Although the two are quite different in structure, there is a similarity
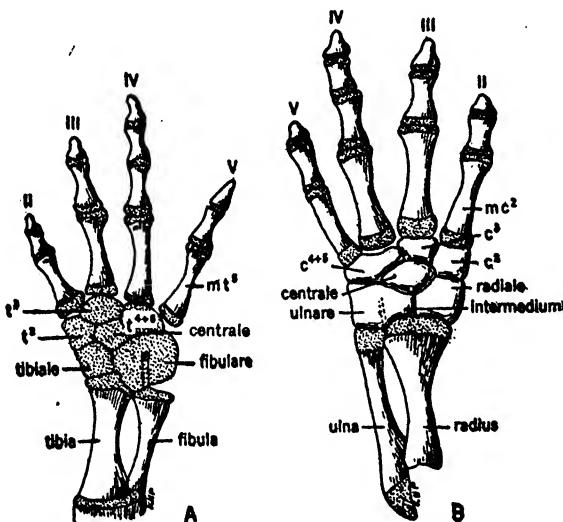
Fig. 117. A, foot of Necturus; B, hand of Necturus.

that suggests a common origin, and it seems probable that the limb ancestry must be sought among the lobe-finned crossopterygians. *Sauripterus* and *Eusthenopteron*, two fossil forms, have so far offered the best opportunity for tracing this evolution. Embryology offers no evidence, and it appears that paleontology must solve the problem, if it is ever to be solved.

The bases of the first fins were imbedded in the body wall, and their evolution required that the bases be lengthened so as to protrude from the body and make motion possible. The lappet-like fins of *Cladoselache* (Fig. 113 *A, B*) could have but little movement, while the extended fin-bases, such as those of *Polypterus* and the older crossopterygians,

were capable of movement similar to that of tetrapod limbs. *Neoceratodus*, the Australian lung-fish, has lost the radials, leaving a series of basal cartilages to support the fin. The elasmobranchs have a con-
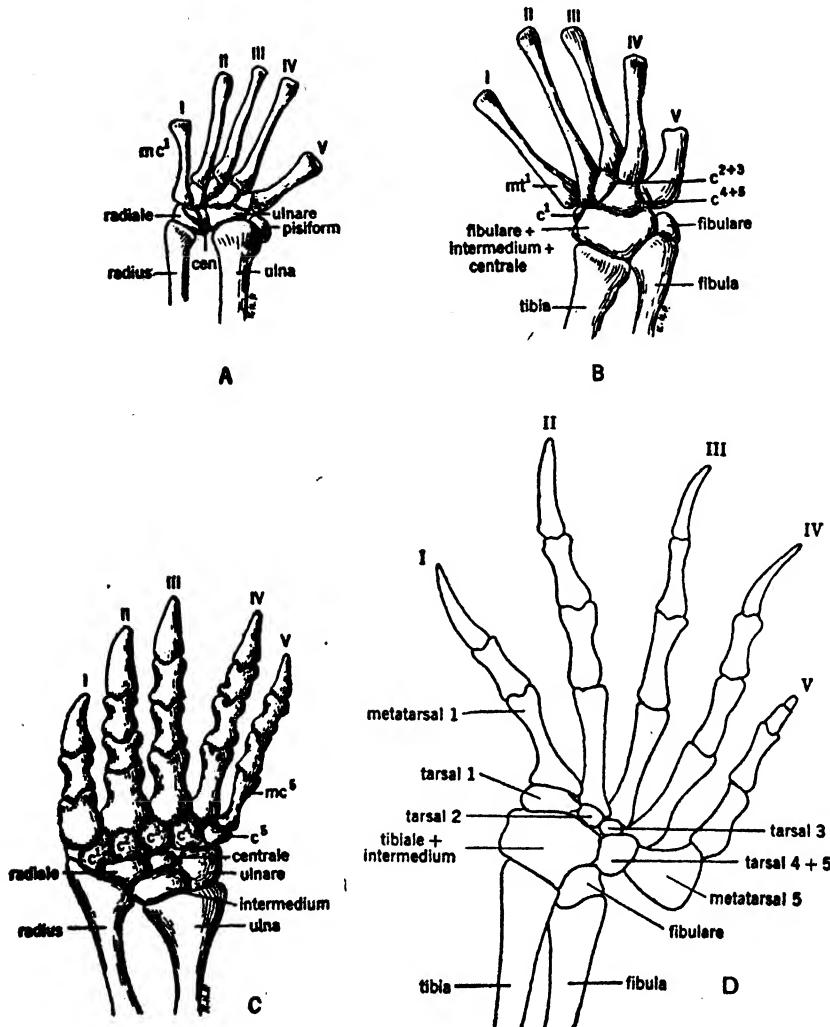
FIG. 118. Vertebrate hands and feet. A, right manus of lizard; B, right foot of lizard (Sceloporus magister); C, right manus of turtle; D, right pes of Pseudemys troosti.

densed series of elements arranged in the anterior fin as three basal cartilages (Fig. 270 *A*, *B*), the propterygium, mesopterygium, and the metapterygium. From these a series of cartilages radiate off, the fin being bordered by horny rays, attached or overlapping the small radials.

The teleosts have a much more condensed fin-base, but the basalia and radialia have been replaced by ossified dermal rays.

There were two possibilities for the development of the tetrapod limb from the fin: first, by the use of the biserial fin of the *Neoceratodus* type, in which there is a main axis with a series of pre- and postaxial radials; and, second, from the type of the fin of the crossopterygian, in which there was no main axis. The lobe-finned crossopterygians seem to supply the most feasible origin, and paleontology offers more evidence for the support of this view.

The first appendages, being at right angles to the body, were not in a position to support its weight. For this reason amphibians and the early reptiles could not sustain the body for any great length of time. With further adaptation the legs of higher reptiles and mammals shifted under the body so that there was a better distribution of the weight and a better mechanical adjustment.

The pattern of the tetrapod limb is surprisingly regular and persistent. The anterior and posterior limbs are made on the same plan, with corresponding elements and a similar musculature.

Segments of the Limbs

The segments of the anterior and posterior limbs, being made up of similar parts, may be compared as follows:

Segment	Anterior limb	Posterior limb
First..................	Humerus (upper arm)	Femur (thigh)
Second..............	{ Radius Ulna } (forearm)	{ Tibia Fibula } (shank)
Third...............	{ Carpus (wrist) Metacarpus (hand) Phalanges (fingers)	Tarsus (ankle) Metatarsus (foot) Phalanges (toes)

The limbs of tetrapods are highly specialized and closely correlated with life habits, all of which react upon the original pattern of the limb. The most primitive type of the foot appears to be the plantigrade, in which the whole under surface is used in walking; a modification, the digitigrade, elevates the posterior part of the foot so that the tarsal or carpal segments do not come in contact with the ground; while the unguligrade, the most extreme type, walks entirely upon the ends of the fingers or toes, which are encased in a horny hoof.

Anterior Limbs

The first segment of the anterior limb is formed by the humerus (Fig. 114), a single element, which articulates proximally with the glenoid fossa of the scapula and distally with the radius and ulna. Its

shape varies with its use in different adaptations. It has an articular head at the proximal end, a shaft, and a trochlear surface distally for the articulation with the radius and ulna. Several tuberosities for muscular insertion develop at the anterior end, and lateral foramina, the ectepicondylar and entepicondylar, may be present at the distal end.

The forearm (Fig. 115), or second segment, consists of two bones, the radius and ulna. In lower forms these bones are much alike, but in the higher, especially mammals, the ability to twist (pronation and supination) becomes highly developed with corresponding changes in the two bones. In animals specialized for running, the two bones are joined to make the segment stronger.

The carpus consists of a varying number of small elements that connect with the radius and ulna proximally, and with the metacarpus distally. Originally the carpals were in three rows, but in modern forms the middle row is absent or consists of but one or two small bones, called centralia. The greatest change in the carpals comes in the shifting necessary to form the mesaxonic and paraxonic (Fig. 116) types of hands and feet. The main axis of stress goes through the third digit in the mesaxonic type, and between the third and fourth digits in the paraxonic type.

Fig. 119. Paddle of a water reptile (Ichthyosaurus). After Abel.
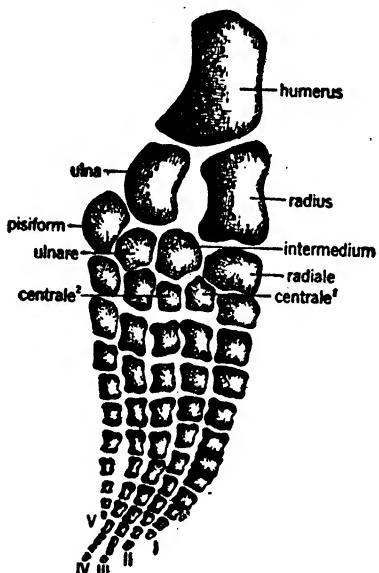
THE BONES OF THE CARPUS, WITH SYNONYMS

	Terms used in comparative anatomy	Abbreviations	Terms used in medical anatomy	Synonyms
Proximal row.....	Radiale	r	Scaphoid	Navicular
	Intermedium	i	Semilunar	Lunate
	Ulnare	u	Triquetral	Cuneiform, pyramidal
	Pisiform	p	(Sesamoid of the ulna)	
Medial row.......	Centrale (0 — 3)	Cen.		
Distal row	Carpale 1	c¹	Trapezium	Multangular major
	Carpale 2	c²	Trapezoid	Multangular minor
	Carpale 3	c³	Capitate	Magnum
	Carpale 4 }	c⁴	Hamate	Uncinate, unciform
	Carpale 5 }	c⁵		
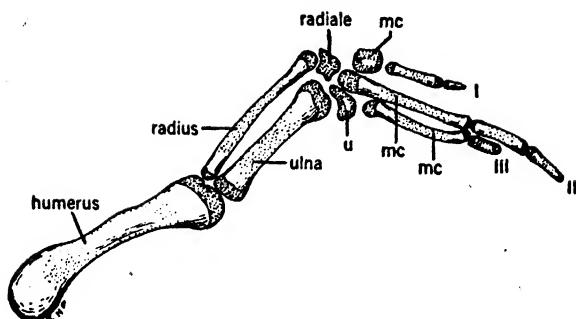
FIG. 120. Right wing of a chicken, just hatched.
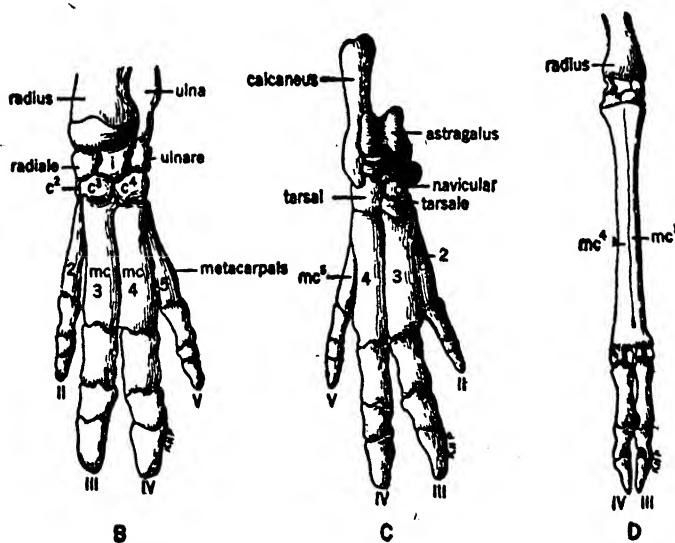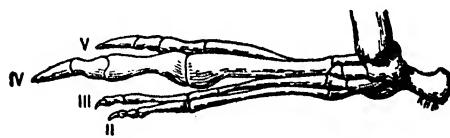
FIG. 121. Manus and pes of mammals. A, right pes of a kangaroo, Dorcopsis (after Abel); B, left manus of pig (after Sisson); C, right pes of pig (after Sisson); D, right manus of antelope.

The metacarpus consists of a series of elongated bones that form the body of the hand. They articulate distally with the digits, and usually equal them in number. Proximally the metacarpals articulate with the row of carpals named carpalia. Primitively the number of carpalia is the same as that of the metacarpals, but there is a tendency for a consolidation of the carpalia especially in carpalia 4 and 5 (Figs. 117, 118, 119, 121, 122).
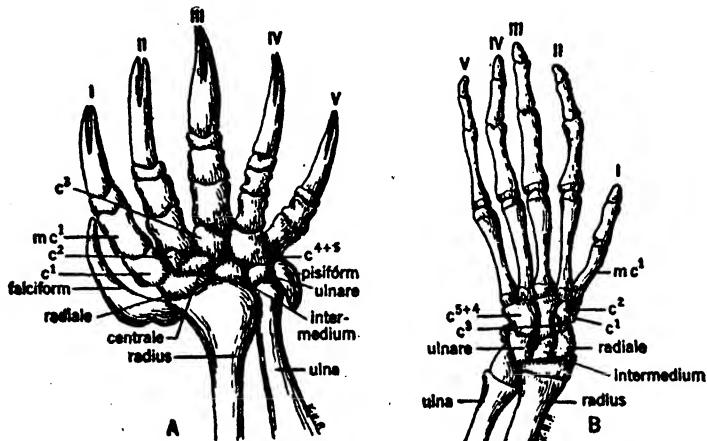
FIG. 122. Mammalian hands. A, right manus of mole (after Weber); B, left manus of monkey (Macacus rhesus).

Posterior Limbs

The posterior limb is generally much heavier than the anterior, for it takes more of the stress and strain in running and jumping. For this reason, adaptive changes, such as loss of toes, are likely to appear first in the hind limb.

The femur (Fig. 123) has a heavy head for articulation with the acetabular socket of the pelvis. Trochanters and muscle insertions may develop on the head and shaft. Articulation with the tibia and fibula is by a horseshoe-shaped surface, and the patella, a sesamoid bone, slides over this articulation.

The second segment (Fig. 124) of the posterior limb consists of the tibia and fibula, the tibia corresponding in position to the radius and the fibula to the ulna. The fibula is variable and may become greatly modified or vestigial.

The tarsus corresponds to the carpus and is made up of a similar series of small elements. Because of the variable use of the foot, there is much modification of these bones, such as shifting in position, joining

with other elements, or dropping out entirely. In mammals there is a decided shift of position in the proximal row of tarsal bones, so that, instead of being side by side, the talus (astragalus) is anterior to the calcaneus (fibulare), which is on the sole of the foot. The talus, or
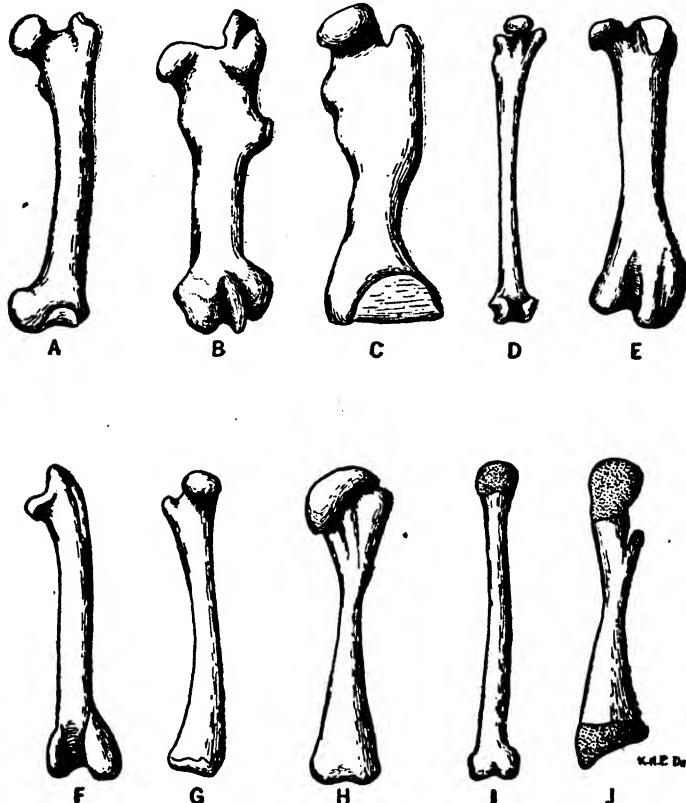
FIG. 123. Series of femurs showing variations in vertebrate classes. A, ape (Orang); B, horse (Equus); C, spiny anteater (Echidna); D, bat (Pteropus); E, pelican (Pelicanus); F, chicken (Gallus); G, horned lizard (Phrynosoma); H, turtle (Chelydra); I, frog (Rana); J, mud puppy (Necturus).

astragalus, is interpreted in several ways as a combination of the tibiale and centrale, or of the intermedium and centrale. The talus, which is flat in the monotremes and marsupials, becomes keeled on the surface which articulates with the tibia, to prevent slipping in this important joint (Figs. 117, 118, 119, 121, 125).
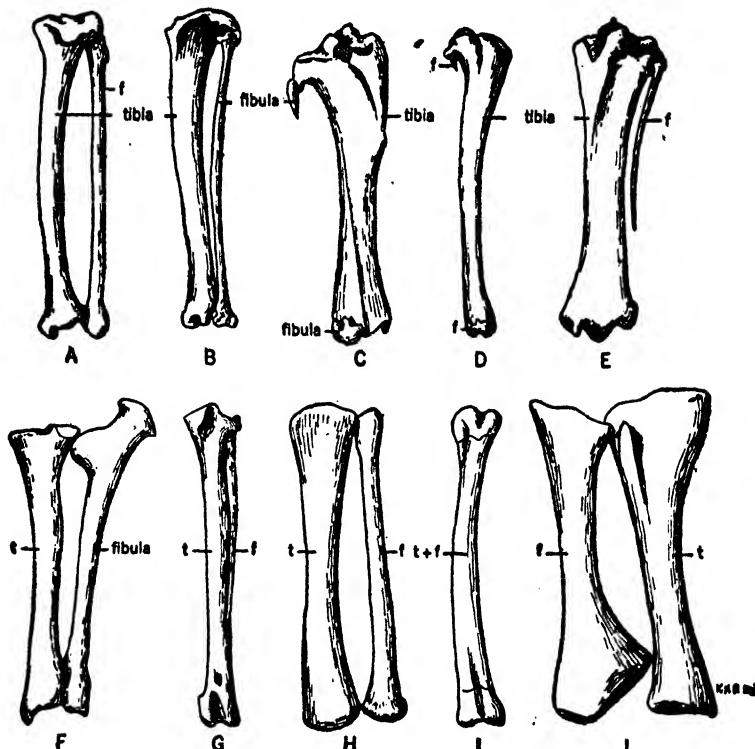
FIG. 124. ' Tibia and fibula in different vertebrate classes, reduced to the same size. A, ape (Orang); B, cat (Felis); C, cow (Bos); D, Antelope (Antilocapra); E, horse (Equus); F, Manis; G, turkey ('Maleagris);' H, alligator; I, frog (Rana); J, mud puppy (Necturus).

THE BONES OF THE TARSUS, WITH SYNONYMS

Terms used in comparative anatomy	Abbre- via- tions	Terms used in medical anatomy
Proximal row..... { Fibulare	f	Calcaneus
Intermedium	i	Talus or astragalus (the same as
Tibiale	t	tibiale + intermedium or inter- medium + centrale)
Medial row ..... Centrale	Cen.	Navicular
Distal row....... { Tarsale 1	t¹	Entocuneiform
Tarsale 2	t²	Mesocuneiform
Tarsale 3	t³	Ectocuneiform
Tarsale 4 }	t⁴	Cuboid
Tarsale 5 }	t⁵	

The metatarsal bones are also elongated elements. They form the articulation for the digits distally and usually equal the number of digits. They articulate with the tarsus, and, although primitively there

was a tarsal bone for each metatarsal, in most animals the tarsalia are reduced either by fusion or by elimination (Figs. 117, 118, 119, 121, 125).

Each digit is made up of a series of phalangeal bones that vary in number but are usually quite regular within the classes. The digits are designated as digits I, II, III, etc. The phalangeal formula becomes quite an aid in classification. The following table gives the phalangeal formula for the manus and pes of a few representative tetrapods. The formula is made up of five terms, referring to the

Fig. 125. Right pes of a bear.

five digits (beginning with the first digit, i.e., the thumb or great toe), and the number of phalanges in each digit is indicated by the numeral. Missing digits are indicated by zero.

PHALANGEAL FORMULA IN REPRESENTATIVE VERTEBRATES

	Manus	Pes
Cryptobranchus	0-2-2-3-2	2-2-3-3-2
Rana catesbiana	0-2-2-3-2	2-2-3-3-2
Chelydra serpentina	2-3-3-3-3	2-3-3-3-3
Alligator	2-3-4-3-3	2-3-4-3-0
Sphenodon	2-3-4-5-3	2-3-4-5-4
Gallus	1-2-1-0-0	2-3-4-5-0
Canis familiaris	2-3-3-3-3	1-3-3-3-3
Sus scrofa	0-3-3-3-3	0-3-3-3-3
Bos	0-0-3-3-0	0-0-3-3-0
Caballus	0-0-3-0-0	0-0-3-0-0
Homo	2-3-3-3-3	2-3-3-3-3

Peculiar Bones

Sesamoid bones are ossified parts of tendons associated with joints in limbs, though not a part of the skeletal system. They form smooth bearings for muscle action over joints. In man the knee cap is a sesamoid, as also is the pisiform element of the proximal row of carpal bones, which articulates with the ulnare by a definite facet. Small sesamoids called fabellae are on the posterior side of the knee joint. A variable number of sesamoids are found on the flexor sides of some joints in the hands and feet.

A few other bones in the body are not connected with the skeletal

system. The os cordis, or heart bone (Fig. 126 *B*), developed in the heart of some ungulates (*Bos*), may be of some size but is irregular and not of a fixed shape. In all classes except the mammals true osseous plates are formed in the sclerotic coat of the eye (Fig. 126 *A*), forming a ring or even a cup. The os priapi, or penis bone (Fig. 126 *C*), is found in the following orders of the mammals: Carnivora, Chiroptera, Pinnipedia, Rodentia, Cetacea, Marsupialia, and lower primates.
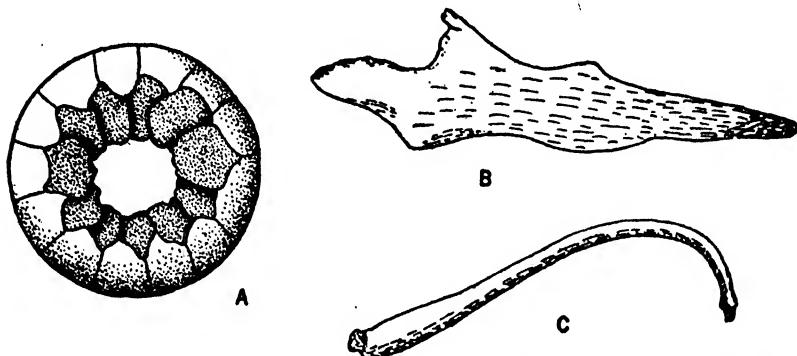
FIG. 126.   Peculiar skeletal elements. A, sclerotic bones of lizard; B, heart bone (os cordis) of cow; C, penis bone (os priapi) of raccoon.

Résumé

An endoskeleton is typical of all chordates. Bones are of cartilaginous and membranous origin. The skeleton of vertebrates consists of three divisions, axial, appendicular, and visceral. The skull or cranium is comprised of the neurocranium, which surrounds the brain and sense organs; the splanchnocranium, which is made up of parts of the visceral skeleton; and the dermocranium, which consists of the investing membrane bones. In the fishes, and also in the embryos of all vertebrates, the chondrocranium originates by the coalescing of cartilages, the parachordals (which parallel the notochord in the ear region), the trabeculae (in the eye region), and the cartilaginous capsules around the sense organs. The bony skull of fishes is developed in several stages: first, dermal plates invest the chondrocranium, as in the sturgeon; second, the chondrocranium begins to be ossified, as in *Amia*; third, the entire chondrocranium becomes ossified, and the dermal plates are closely united to it, as in the teleosts. The skull of amphibians is platybasic, has two condyles, and is much simplified, as compared to fishes, by the reduction of the bones used in connection with respiration. The skull of reptiles is tropibasic, typically has one condyle, loses a few of the amphibian elements, and introduces some new bones. The skull of birds is reptilian in type, but most of the bones are fused together. The mammalian skull has a larger brain case than that of the reptiles; it has two condyles and a temporal complex composed of a number of bones including the otic capsule (which encloses

the ear ossicles). The squamosal portion of the temporal complex forms the new articulation for the mandibles. The dentary is retained as the lower jaw. The quadrate of the reptile becomes the incus, and the articulare becomes the malleus. The teeth are in sockets and consist of incisors, canines, premolars, and molars. Teeth are present only on the premaxillae, maxillae, and dentaries. The visceral skeleton, complete in the fishes, suffers a gradual reduction in land animals. The axial skeleton, starting with the notochord, is replaced by vertebrae, which become specialized in each of the five regions — cervical, thoracic, lumbar, sacral, and caudal. Ribs are of two kinds: the haemal (or fish) ribs, which are sub-peritoneal; and the pleural ribs, which are intermuscular. Originally, ribs were along the entire vertebral column. The sternum appeared first in amphibians. The episternum is found in amphibians, reptiles, and monotremes. Gastralia, or abdominal ribs, were present in primitive amphibians, reptiles, and birds, and are found in some modern reptiles. The three main theories for the origin of limbs are the "gill-arch," and "fin-fold" theories, and the external gill theory of J. Graham Kerr. The anterior, or pectoral, girdle consists primitively of three bones, the scapula and two or more coracoids, but only the scapula remains in mammals except in the monotremes. The clavicle, a dermal bone, may be present. The pelvic girdle consists of three elements: the ilium, pubis, and ischium, with an additional epipubis in marsupials. Tails of fishes have the following forms: diphycercal, heterocercal, homocercal, and gephyrocercal. The tetrapod limb probably was derived from the fin of some lobe-finned crossopterygian. Sesamoid bones, such as the patella and the fabellae of the knee, are ossifications in tendons. An os cordis is found in ungulates, and an os priapi is characteristic of certain mammalian orders.

CHAPTER V

MUSCULAR SYSTEM

The muscular and skeletal systems are closely associated and should be considered together in their proper relations. Bones to which muscles are attached show very clearly the results of muscle pull, and no other influence has so much to do with the configuration, shape, or position of bones. In fact, bones and muscles develop together, since there is such a close correlation between the two. Limb bones in which the muscles have atrophied, either naturally or experimentally, are quite different from those that have developed normally, showing not only a reduction in size but also a decided difference in the developments associated with muscle pull.

Muscle is built up by a multiplication of cells that have the ability to contract and relax under nervous stimulus. Each cell is a complicated unit made up of a nucleus and numerous branching fibrils, surrounded by a wall, the sarcolemna, and filled with a fluid, the sarcoplasm. These units in turn make up bundles and finally individual muscles, which, in connection with the skeletal system and other parts, make movement possible. No proper interpretation of the muscular system can be made without consideration of the skeleton, since processes, ridges, trochanters, and spines all show the influence of muscle pull. Muscular tissue is mesodermal in origin and is found in every part of the body except the nervous system.

Three types of muscle fibers are differentiated: (1) striated muscle fibers make up the general musculature under conscious control; (2) smooth, non-striated muscle fibers are found in the digestive tract and other parts of the body where direct control is impossible, and they are innervated by the autonomic system; (3) the striated muscle fibers of the heart are not under conscious control, but are innervated by the autonomic system and are peculiar in that they are still able to function after all nerve connections have been cut.

The shape of a muscle depends on the work that it has to do and on its point of origin and its point of insertion. Thus sheet muscles, such as the' diaphragm, separate cavities; fusiform muscles found in the limbs are in positions where only a small space is available for origin and insertion and where mechanical problems demand nothing more; triangular muscles, such as the trapezius, appear where there are broad

faces for insertion or origin; and fan-shaped muscles, such as the pectoralis major (Fig. 127) have extensive origins and rather limited insertions. The muscles of the intestinal tract consist of two types, one circular and the other longitudinal. Sphincters surround openings, such as the mouth, eyes, and anus.

Muscles may end in tendons or aponeuroses, or both, thus reducing the bulk but not the strength. Aponeuroses are broad sheets of fibrous connective tissue joining muscles together. The advantage of tendons is striking in the wrists and ankles, where the tendons carry the muscular force to the hands and feet. Parts of tendons may become bone, as in the legs of birds, or they may develop sesamoid or tendon bones (patella of the knee and smaller sesamoids of the hands and feet).

Fascia, a kind of connective tissue which forms a smooth, tough envelope for each muscle and binds groups of them together, plays an extremely important part in the muscular system, since it permits motion with almost no friction. It also forms aponeuroses and blends with tendons and ligaments to facilitate their action. Muscle action is often associated with ligamentary loops (Fig. 128) through which tendons work, as in the flexion of the fingers and toes, where this device makes possible a strong action in a series of hinge joints.

The origin of muscular tissue is in the myotomes; hence all the body musculature is primarily segmental. As the vertebrate body develops, the myomeres gradually approach the mid-ventral line, where they stop at the linea alba. Myosepta divide the muscles into metameric elements, each supplied with a metameric nerve from its region of the spinal cord. Whenever a muscle migrates, it is followed by its original nerve, and it is rare that this connection is changed or lost. A horizontal septum separates the muscle mass into an epaxial, or dorsal, mass and a hypaxial, or ventral, mass. The lateral line of fishes is on the line of separation.

Muscles are generally arranged in pairs, thus forming opposing sets, and this arrangement is necessary because their only action is contraction. A few muscles are sufficient for a simple movement, but a much greater number is required for a wide range of movements. The application of power falls into the three classes of leverage: the first is illustrated by the skull on the neck vertebrae, the second by the pull of Achilles' tendon on the heel, and the third by the pull of the biceps on the forearm (Fig. 129).

Muscles are extremely variable, assuming many forms, often shifting their original position and migrating to new ones. The stapedius muscle of the ear seems to be a slip of the second levator of the gills that has split off and followed the stapes into the ear. There has been

much splitting of muscle masses.　For example, the levator muscle of the fish becomes the adductor mandibularis, which in turn splits into the masseter and temporal, each of which may split again.　The internal

masseter

transverse mandibular

digastric

mylohyoid

sternohyoid

sternomastoid
clavotrapezius
atlanto-scapularis
omyhyoid
acromiodeltoid

atlanto-scapularis
omyhyoid
sternothyroid

superficial pectoral

subscapularis
biceps
teres major
triceps

extensor carpi rad. long.
flexor carpi radialis
pronator teres
flexor digitorum profundus
palmaris longus
flexor carpi ulnaris
latissimus dorsi
deep pectorals

latissimus dorsi

intercostals

external oblique abdominal

rectus abdominis

gluteus superficialis anticus
vastus lateralis

rectus femoris

rectus femoris
vastus medius
gracilis anticus

pectineus
vastus medius
abductor magnus
popliteus
abductor longus
flexor digitorum longus

gastrocnemius
tibialis posticus

flexor fibularis

semitendinosus
semimembranosus
gracilis

Fig. 127.　Ventral musculature of a wood rat.　Redrawn from Howell.

and external pterygoids appear to have split from this adductor mass. The digastric is a muscle of two origins, as shown by the double innervation, the anterior belly innervated by a branch of the trigeminus and the posterior belly by the facialis.　Combinations of muscles gen-

erally show a tendinous area, the inscriptio tendinea, where the joining has taken place. The rectus abdominis shows these inscriptions very clearly.

One of the striking modifications of muscle tissue is its development into an electrical organ in some of the fishes, such as the electric rays, eels, catfishes, and some other teleosts. The electrical areas of these fishes are made up of modified muscle cells, supplied with a heavy innervation, from the spinal or cranial nerves. Some fishes are able to give an electric shock capable of stunning medium-sized animals.

Muscles function not only in movement but also in support of the skeleton, and in this they are very important. A difference in muscular tonus reacts quickly on the animal, and it is easy to note the difference in the carriage and attitude of an animal in perfect condition and one
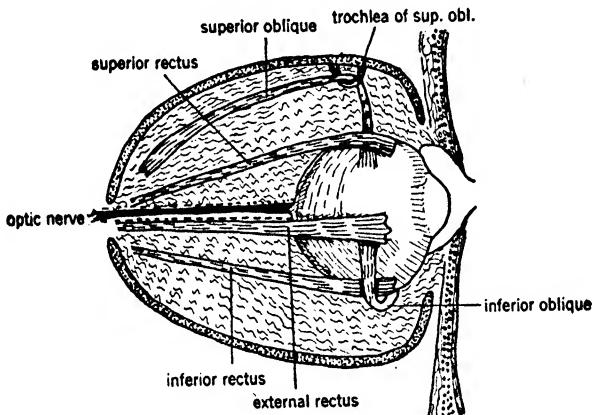
FIG. 128. Eye muscles, showing pulley arrangement of superior oblique. After Plate.

weakened by disease. The shoulder and pelvic joints, while bound by ligaments, are also well secured by the muscular attachments. In describing the action of a muscle, it is sometimes necessary to take into consideration the different positions of the structures concerned, for the action may vary with the position of the part. The contraction of a muscle may have a single definite effect when acting alone, but quite different effects when acting in combination with others. Most movements are the effects of several muscles acting in combination.

The origin of a muscle is generally its attachment to a fixed part; its insertion is on a structure to be moved. These criteria usually make it easy to determine the origin and insertion, but in some cases both the origin and insertion are on movable parts, as in a number of the head muscles in snakes, and here it is necessary to make comparisons with forms in which specialization is not carried to an extreme. The dia-

phragm of mammals originates from the thoracic walls and ends in a
central aponeurosis. Both origins and insertions may be complicated
by splitting, so that they are multiple, as in biceps, triceps, quadriceps,
etc.

In judging the homology of muscles in different classes of vertebrates
a number of criteria are used, but no one is certain. The origins and
insertions may change, muscles may drop out altogether, and sub-
divisions or splittings may occur. Generally the innervation can be
trusted, although its interpretation is often difficult and sometimes
doubtful.

To understand the muscles of the head region, it is necessary to
study the embryology of the structure, since in the adult the original
condition is so masked that any satisfactory interpretation is impos-

Load	Fulcrum	Pull	Fulcrum	Load	Pull	Load	Pull	Fulcrum
	First Class			Second Class			Third Class	
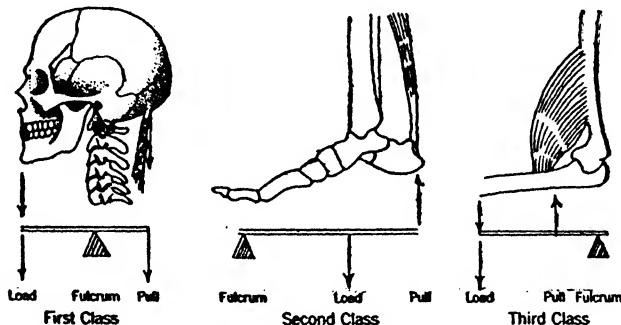
FIG. 129.   Diagram of levers and their relation to muscle pull.   From Morris
after Testut.

sible. The head myotomes show a premandibular series of three
somites and a postmandibular series of a variable number. The dorsal
parts of these myotomes disappear, because skull developments make
them unnecessary. It is probable that at one time each myotome was
served by a segmental nerve, but shifts in the arrangement of this
primitive innervation have been caused by combinations of several
nerves into a single element, such as the vagus, which undoubtedly
represents a number of segmental nerves joined together. Thus three
premandibular myotomes supply the eye musculature: the first myo-
tome forms the superior, inferior, and internal recti and the inferior
oblique — all innervated by the oculomotor nerve (III); the second
myotome forms the superior oblique and is innervated by the trochlear
(IV); the third forms the external rectus and is innervated by the
abducens (VI). The sixth nerve has shifted its influence to a myotome
anterior to its original embryological position.

The growth of the myotomes into the limb buds also shows a shifting of muscular material (Fig. 130). In the developing fins of sharks, a number of buds from the myotomes with their segmental nerves force their way into the developing limb, bifurcating to supply the mesial and lateral sides. There is a wide variation of the number of myotomic buds concerned in the building of the appendicular musculature, and this explains their peculiar innervation and nerve plexus. The muscular sheets of the body wall (Fig. 131) are so arranged that their fibers extend in different directions, thus giving added strength and great powers of compression.

The musculature of the fishes is strictly segmental in character, except in the regions of the head and in the pectoral and pelvic fins. In general the musculature is rather simple but shows some of the specializations that are to occur in the tetrapods. The head musculature is well differentiated in the teleosts and may be highly specialized. The myotomes are retained very distinctly except where they are distorted to permit the muscles of the fins to reach the inner parts of the pectoral and pelvic girdles. The muscles of the fins are

FIG. 130. Diagram showing the formation of limb buds. A, adult condition, with muscles and nerves artificially spaced to show relations. B, adult condition with muscles and nerves naturally grouped. After Goodrich.

beginning to encircle the body, both dorsally and ventrally, thus partially covering the original myotomic system. The horizontal septum, with its lateral line, still separates the body muscles into an epaxial, or dorsal, series and a hypaxial, or ventral, series. Similarly the dorsal musculature of the skull consists of a series of muscles to close the jaw, and there is also a single ventral muscle, the digastric (Figs. 132, 133), which operates with the throat muscles to open the jaw. The skull is attached to the vertebral column by ligaments and a connecting musculature that is formed from several modified myotomes.

The muscles of the higher animals tend to become specialized, and

their original myotomic arrangement is lost except in a few cases, such as the serratus magnus and the rectus abdominis. Their original relations may be indicated through their innervation, although migrations and splittings have often completely changed their original position.

The musculature of the head region is developed to assist in the movement of the gills (Fig. 134), with their arches, since a fresh supply of water must flow constantly over the gill lamellae. The branchial musculature is divided into a series of depressors and levators, all of which have been derived from the original segments of the head and body region. The origin of the muscles is linked with the number of head segments, usually considered as one pre-oral and eight post-oral, the
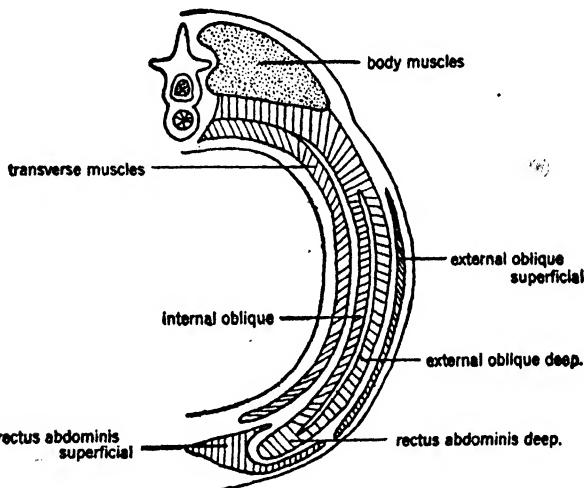
FIG. 131. Cross-section of body wall to show musculature. After Bütchli.

pre-oral probably representing a combination of several segments. These regions are marked by the cranial nerves and their branches. The innervation of the depressors and levators is through the cranial nerves, the mandibular segment by the trigeminus, the first branchial by the glossopharyngeal, and the remaining four branchials by the vagus. These rather simple muscles, superficial in position, serve the fishes for the regulation of the arches. The gills of the sharks are supplied with a musculature that gives considerable movement to the individual gill arches. The dorsal and ventral constrictors raise and lower the gills; within the individual gill arch, a series of small muscles — the interarcuales, the adductor arcuus branchiales, and the interbranchiales — give further action. The ventral region of the gill arches has a number of long muscles connecting it with the mandibles and the coracoid carti-

lage. Both the coraco-mandibularis and the coraco-hyoideus assist in movement of this basal region by tensing or relaxing the ventral wall.

The highly specialized musculature required for the movements of the gills in fishes is much simplified or lost in the land tetrapods. Here the muscles corresponding to those in gills form adductors, or closing muscles, of the jaw. The simple adductor becomes subdivided, usually forming a masseter and a temporal for levators (Figs. 127, 133, 135). A ventral depressor mandibulae, or digastric muscle, opens the jaw (Figs. 127, 132). Lateral and anterior movements are made possible by different combinations of these muscles, assisted by two small muscles, the pterygoid externus and internus. A broad sheet of muscle, the mylohyoid (Fig. 127), extends between the mandibles, acting as a
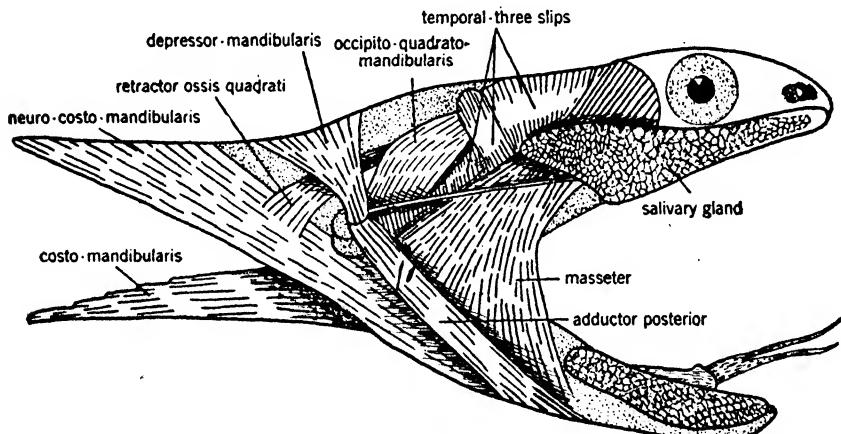
Fig. 132. Musculature of snake head (Natrix).

constrictor for the throat by raising the floor of the mouth. The musculature of the tongue becomes highly specialized in tetrapods, by the development of an intrinsic musculature which gives movement in all directions. The hyoglossus, genioglossus, styloglossus, and other muscles assist in its action. In the throat region, besides the external muscles, there is a series connected with the hyoid structure, the genio-hyoids, sternohyoids, thyrohyoids, and omohyoids (Figs. 127, 136).

The skull is attached to the cervical vertebrae by ligaments and also by a series of muscles, some short and some long, that assist in holding the head in position and in giving it freedom of movement. These short muscles are the rectus capitis and the oblique capitis, which originate on the atlas and axis. The longer muscles are the longissimus capitis, semispinalis capitis, and the splenius capitis, which originate on the cervical vertebrae and are inserted on the occipital region of
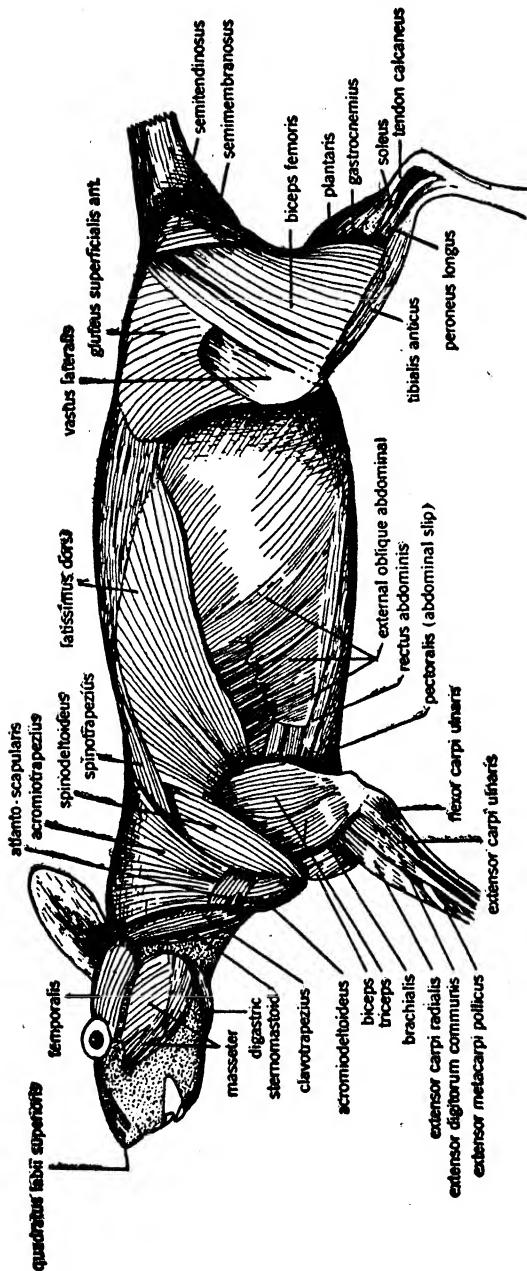
FIG. 133. Lateral muscles of wood rat. Redrawn from Howell.

the head. Superficially, the large posterior trapezius connects the skull with the clavicle and scapula (in man), and more anteriorly the sternomastoid and cleidomastoid connect the sternum and clavicle with the skull (Figs. 133, 135).

The spinal column is supplied with a series of short muscles between individual vertebrae and with a series of longer muscles between the regions of the column. Besides the vertebral system proper, there are series of muscles connecting it with other movable parts, such as the girdles and limbs, and series of intercostal muscles between the ribs to assist in breathing.

In the lower tetrapods the pectoral girdle may be closely articulated with the sternum through the coracoids and clavicle, but in the mammals the connection of the girdle is entirely by ligament and muscle, except in those forms in which a clavicle is present. (In these mammals the clavicle connects the scapula and the sternum.) By means of the large superficial trapezius muscle, the scapula is attached strongly to the vertebral column and also to the skull. In addition the scapula is moved by a series of muscles that connect it with the body, such as the levator scapulae, serratus magnus, and the rhomboid series (Figs. 133, 135). These working in combinations elevate, depress, adduct, and abduct the scapula, so that the musculature is admirably adapted to give a maximum of movement in the shoulder joint. Since both the purely scapular muscles, as well as the humeral muscles, are concerned in the movement of this part of the fore limb, the number of muscles in this region is large.

In the segments of the anterior limb, flexion, extension, adduction, abduction, circumduction, pronation, and supination are possible. The extension of the humerus is through the triceps on the posterior side of the arm, and flexion by the biceps, deltoid, and coraco-brachialis. Adduction, abduction, and medial and lateral rotation are made possible by the teres major and minor, subscapularis, latissimus dorsi, and pectoralis major, in different combinations (Figs. 127, 133). The pronator and supinator muscles act between the radius and the ulna.

In animals that make much use of their fore limbs, the forearm-carpus segment becomes highly specialized, with a wide differentiation of the musculature to the individual digits. Muscles extend to the carpus and also to the digits by means of tendons that reach to the finger tips. Although the muscles have fleshy origins on the upper arm and forearm, only tendons are extended to the hand and fingers, thus keeping the wrist small and pliable. The extensor digitorum communis sends tendons to fingers 2, 3, 4, and 5, and additional extensors go to fingers 1, 2, and 5. The flexor digitorum sublimis is

inserted on the proximal joints of the fingers; the flexor digitorum profundus, a deeper muscle, is inserted on the proximal ends of the third row of phalangeal bones. Besides the large extensors and flexors, smaller muscles are supplied to the fingers, giving them strength and a greater variety of movement, as well as support, especially in the extended position.

The musculature of the posterior girdle consists first of muscles that are associated with the pelvis and the vertebral column, and secondly with the femur and other segments of the posterior limb. Both groups are concerned in the flexion and extension of the pelvis. These movements are accomplished by working the muscles singly or in pairs. The principal muscles concerned in the flexion of the pelvis are the gluteals, hamstring muscles, and the abdominals. The extension
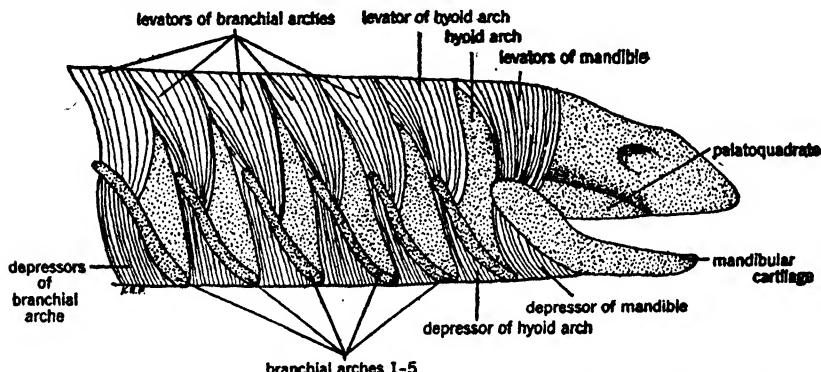
FIG. 134. Primitive musculature of head region. Redrawn from Wilder.

group consists of the iliopsoas muscles, the adductors, quadriceps extensor, sartorius, and gracilis. Rotation is effected by different combinations of these muscles (Figs. 133, 137).

The muscles of the femur, although not so great in number as those of the humerus, permit extension, flexion, adduction, abduction, rotation, and circumduction. The main muscle concerned in extension is the gluteus maximus, and in flexion the iliopsoas and pectineus. The abductors are gluteus maximus, gluteus medius, and gluteus minimus, piriformis, and tensor fascia; adduction is effected by the adductor longus, adductor brevis, and adductor magnus assisted by the pectineus and obturator externus (Fig. 137). Rotation of the femur is through combinations of these muscles, together with the action of the gemelli and quadratus femoris.

The action of the knee joint consists principally of flexion and extension, with but a limited amount of rotation. The extension is

through the large quadriceps femoris, which consists of the rectus femoris and the three vasti muscles (Fig. 137). These end in a tendon which is attached to the proximal end of the tibia. Included in this tendon is the large sesamoid bone, the patella. The flexors of the leg are numerous, consisting of the biceps, popliteus, sartorius, gracilis, semimembranosus, and semitendinosus (Figs. 127, 137). Amphibia and reptiles
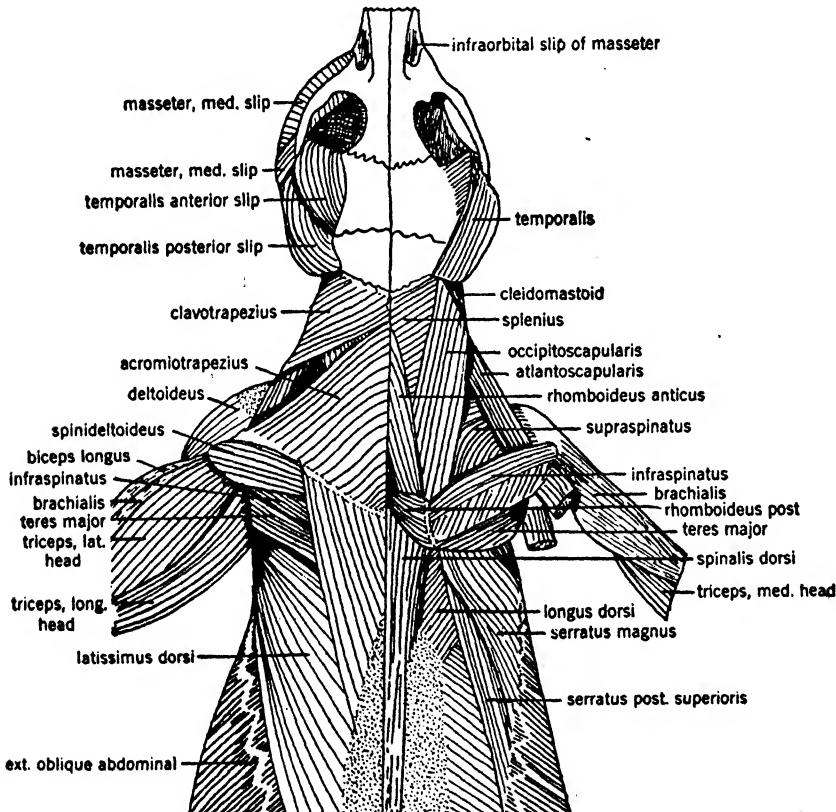
FIG. 135. Dorsal musculature of head and shoulders in wood rat.
After Howell.

have possibilities of more rotation between the tibia and fibula than the higher animals, in which there is a tendency to ankylosis of the fibula with the tibia, with a reduction or almost complete loss of the fibula.

Because of the importance of the ankle joint, it is supplied with a very highly specialized musculature. Here the extensor muscles are the gastrocnemius, soleus, and plantaris, which unite to form the tendon of Achilles, and the tibialis posterior, peroneus longus, and peroneus

brevis (Figs. 127, 137). Flexion, which is a weaker action, is through the peroneus tertius and tibialis anterior, and the extensors of the toes. The tibialis posterior and the three peroneus muscles are concerned in rotation, inversion and eversion of the foot.

There is a striking resemblance between the musculature of the foot and that of the hand. The foot is supplied with the usual possibilities of movement in animals in which there is no reduction of the digits, but
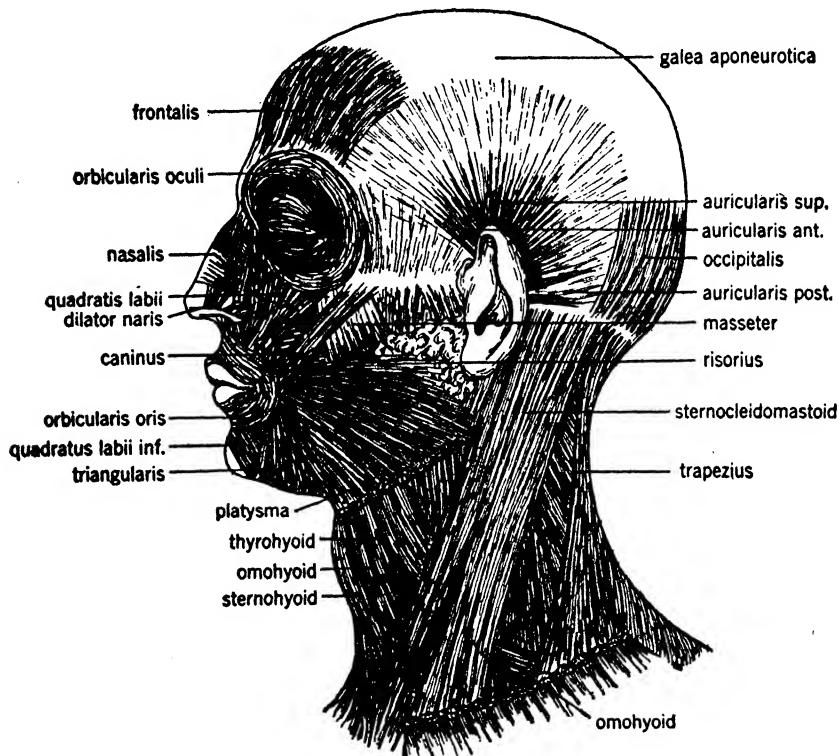
FIG. 136. Lateral muscles of human head. Redrawn from Morris.

in those with fewer toes there is a tendency to restrict the movements for mechanical reasons. Usually there is a possibility of rotation in the first and fifth toes when they are present. The extensor digitorum longus originates on the proximal end of the tibia, forming tendons at the ankle which supply all but the first toe, this being supplied by the extensor hallucis longus. A shorter muscle, the extensor digitorum brevis, originates on the calcaneus and acts as a short extensor. The toes are flexed chiefly by the flexor digitorum longus, which extends through four tendons to toes 2, 3, 4, 5. These same toes are also flexed

by the flexor digitorum brevis.   The first toe, or hallux, is flexed by
flexor hallucis longus and brevis.   The fifth toe has an additional muscle,
the flexor digiti quinti brevis.   Toes 1 and 5 have the greatest move-
ment since they have some rotation.   In apes there is considerable
opposability of the hallux, but in man this character is reduced or lost.

The musculature of the feet varies greatly, because of the different
ways in which they are used.   In flat-footed plantigrade animals, which
walk on the whole sole of the foot, there is great pliability in the individ-
ual parts, and often a tendency to form a bifurcate structure, in which
two parts are opposed for grasping.   Though plantigrade in structure,
the foot of man is used to raise him on his toes in many activities.   The
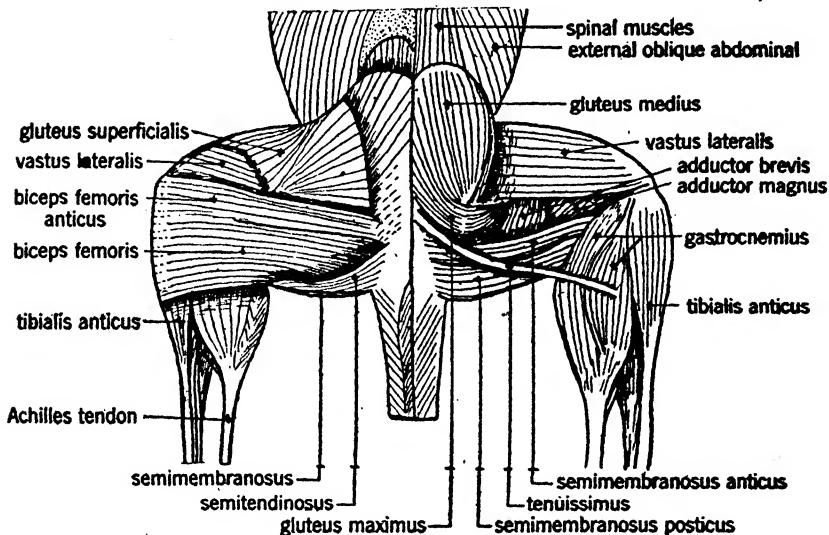
FIG. 127.   Dorsal rump muscles of wood rat.   After Howell.

digitigrade foot loses its independent action of the toes to some extent,
and there is a corresponding simplification in the musculature.   In the
unguligrade foot, such as that of the horse and cow, the musculature is
still more simplified and specialized, and the foot is greatly strengthened
by reduction of lateral movement.

Besides the musculature of the skeleton a system of superficial muscles
is connected with the integument that moves the skin.   Within the
skin structure, small muscles in the corium move structures such as
scales, feathers, and hairs.   These are under the control of the auto-
nomic system.   In the region of the neck and face a superficial muscle
layer, the sphincter colli of the reptiles and birds, acts to move the skin.
In the higher animals it becomes much specialized and divided into a

superficial platysma and a still deeper layer called the sphincter colli. From the outer sheet, the platysma, the facial musculature is developed, consisting of muscles that are concerned in the movement of the ears, eyelids, nose, lips, and scalp. This system is highly specialized in mammals and extremely well developed in man and other primates. A second superficial system, known as the panniculus carnosus, is supposed to be a derivative of the latissimus and the pectoralis muscles. It may spread over the whole body or may be limited to the region of the axilla of the fore leg and the inguinal region of the hind leg. Its function is to enable the animal to shake the skin vigorously, to expel water, insects, or other foreign material from the skin and hair. The armadillo and manis make use of the sheet for rolling themselves into a ball.

Résumé

The muscular system is very closely associated with the parts of the skeleton. The dynamic units of the system are contractile cells, which are united into groups, forming bundles and eventually muscles. The tough, smooth tissue that ties the bundles together and sheathes the muscles is called fascia. Striated muscles, except those forming the heart, are under the control of the central nervous system; unstriated muscles are under the control of the autonomic system. Muscles may be fusiform, fan-shaped, triangular, sheet-like (diaphragm), or circular (sphincters). They are usually arranged in opposing pairs and always work according to one or another of the three classes of mechanical leverage. A muscle may shift its position and migrate, or it may split into several slips, or it may join with another muscle in a new relationship. The innervation of muscles, however, is usually constant, and a muscle of two origins retains a double innervation (digastric). Muscles, in general, keep the innervation of the myotomes from which they originate. The myotomic arrangement of body muscles is retained in fishes and amphibians but is lost or not apparent in higher vertebrates. In some fishes (electric ray, eel, etc.) parts of the muscular system are developed into electrical organs. Muscles usually have an origin on a fixed part of the skeleton and an insertion on a movable part. The insertion may be by direct attachment or by means of fascia forming an aponeurosis or by a tendon. Muscles do not cross the midline of the body. The most complicated musculature is that of the girdles and limbs, where a maximum of movement is necessary. Small muscles in the skin move the hair, feathers, and scales. By means of the panniculus carnosus some animals may move large sections of the skin.

CHAPTER VI

DIGESTIVE SYSTEM

The digestive system is one of the earliest to develop, since the processes of food absorption are necessary for differentiation and growth. Early in the development of the embryo there is a differentiation of the ectoderm, or protective layer, and the endoderm, or digestive layer. Primarily, the digestive system consists of a simple tube, of which the ends, the mouth and rectum, are lined with ectodermal tissue and the rest with endodermal tissue. In the process of development, certain outpocketings occur which may be concerned in the digestive functions or may be associated with other activities of the body. The greatest problem of the system is to keep the absorptive area large enough to supply the bulk of the animal with sufficient food material, and for this reason the tube is never straight except in the simplest vertebrates.

Since the processes of digestion are very complex and since so many kinds of foods are used, there is much specialization of the parts to supply the area required for different activities. Even the simplest animals have a mouth where the food is received, a stomach for the storage and action of the gastric juices, an intestine for further elaboration of the digestive processes and absorption into the venous system, and finally a posterior differentiation of the gut for the reduction of the waste by the removal of the excess water.

The processes of digestion consist for the most part of the simplification of the different complex foods utilized, since it is by this action that the materials are changed chemically so that they are simple enough to be absorbed by the cells of the body. Glands are located in most regions of the tube, the largest being the liver and the pancreas, which have so increased in size that they have withdrawn from the wall of the intestine and are now connected only by ducts. The general innervation is through the vagus nerve and the autonomic system.

The digestive activities may be divided into four main heads: (1) mechanical breaking up of food, (2) chemical changes, (3) absorption, and (4) assimilation; and for each of these there are anatomical adaptations.

The mechanical reduction of food is best accomplished in the mouth of animals that have teeth. If teeth are missing, as in birds and turtles, the food may be torn to pieces by jerking and tearing. In some turtles

the esophagus is horny and thus assists in the reduction process, but by far the most effective arrangement in toothless animals is the division of the stomach into a glandular portion, or proventriculus, and a gizzard lined with a horny epithelium, which grinds the food to a pulp by means of stones or grit. Such gizzards are found in some reptiles and birds. By means of circular and longitudinal muscles in the walls of the stomach and intestine, peristaltic movements extend along the digestive tract, gently churning the food in the stomach and keeping it moving through the entire tube.

The second stage, or digestion proper, consists of chemical processes by which foods with a complex structure are rendered simple. Special enzymes, such as invertase, ptyalin, lipase, amylopsin, and pepsin, act as catalyzers; that is, though these enzymes may take no active part in digestion, their presence is necessary for the process. The sources of digestive juices are the mouth, stomach, small intestine, liver, and pancreas, the last two contributing their products to the small intestine. The large intestine is generally not the seat of digestive action, although digestion of cellulose may take place there in animals eating food made up of this material. The reduction in this case is bacterial.

The main absorption of food takes place in the small intestine, although a slight amount may be taken from the walls of the stomach and also from the proximal end of the large intestine. The absorption into the blood is through the villi (Fig. 145) which line the walls of the small intestine, and from these the digested food is conducted through the veins of the mesenteries to the hepatic portal system and the liver. As the blood passes through the capillaries of the liver, a part of its load of food is stored there, so that the general food content of the blood circulating over the body remains somewhat constant. Sugars thus extracted from the blood by the cells of the liver are stored as glycogens for future use. (The kidneys also serve to regulate the sugar content of the blood by taking out any large surplus.) The fats are taken from the small intestine into the lymphatic system through the villi or through Peyer's patches and are put into the venous blood stream through the thoracic ducts. (See the chapter on the circulatory system.)

The assimilation of food by the cells of the body is not possible until the blood is taken into capillaries where the plasma carrying the food can escape and come in direct contact with the cells themselves. From this plasma the individual cells are able to take up the material that they need and make it a part of themselves.

Mouth. — The mouth of the chordates appears to be a new structure, not homologous with the mouth of the invertebrates, and there is some difference of opinion as to whether the mouth of the vertebrate is the

same as that found in the protochordates.   As an entrance way to the digestive system, the mouth is subject to a great deal of variation, since in fishes it is so closely correlated with water respiration, while in tetrapods it is associated with the action of the lungs.   The ectodermal lining extends to the region of the pharynx.   There are few glands in the mouths of fishes, but there is a progressive increase in these glands, as the land forms become more stable, and the mouth takes a more important part in the preparation of food.   The mouth of cyclostomes is jawless and supplied with horny, rasping teeth that aid in their peculiar type of food-getting.   The fish mouth is loosely organized, and roofed with a number of dermal bones, all of which may bear teeth.   The teeth vary with the food, being absent in herbivorous forms and sharp and needle-like in the carnivorous types.   (See Chapter III.)   Some have crushing plates formed either by the teeth or from the pharyngeal series. Whereas the roof of the mouth is fairly compact, the sides and the floor are likely to be a loose series of bones with a maximum of movement. The large gill slits open into the pharyngeal region, but this gap is closed by the gill-rakers, which help to direct the food into the esophagus. Numerous deformed fish, in which the mouth has been destroyed by accident, are able to live and maintain a fair metabolic balance.   A carp in which the mouth had been completely closed by the bite of some predator (turtle?) was taken from the Illinois River last season, and although somewhat dwarfed, was in a surprisingly good condition, considering the fact that all the food had to enter by way of the gill slits. Since the food is generally gulped down, no special apparatus for grinding food is needed in the carnivorous fishes.   Herbivorous types, however, may have special grinding pads, the carp having a horny pad developed in the basioccipital that works in against the large pharyngeal teeth.   Similar opposing plates are developed in the pharyngeal series of the fresh-water drum, *Aplodinotus grunniens*.   Mouth glands and tongue are of little use in fishes.

The amphibian mouth is more compact, since even in the urodeles there is a reduction of the gill structure and a closer association of the working parts of the jaws.   There is the new connection between the nose and the mouth — a condition that requires special consideration in the Amphibia as well as in other tetrapods.   There is a rapid increase in the number and types of glands, since lip, tongue, intermaxillary, choanae, and throat glands may be present.

The mouth of reptiles is more compact than that of the Amphibia, but there is still some looseness of the skeletal structures.   Since the food is usually gulped and swallowed, the jaws and teeth serve principally for seizing and holding wriggling prey.   The entrance of the posterior

nares is on the roof of the mouth in all but the Crocodilia, where the palatines and maxillae meet on the midline of the roof and force the nares back to the pharyngeal region.   Mouth glands become very prominent and are used primarily for lubrication, with the exception of venom production in the poisonous snakes and in the poisonous lizard, the Gila monster (*Heloderma*).

The mouth of birds is similar to that of the reptiles, since little action takes place, except for a slight moistening and lubrication of food.   The glands are well developed in the grain-eaters and reduced in the carnivorous and water types.

The mammal mouth has the best separation from the nasal passage, since the hard palate is well developed and prolonged to the posterior, so that the air is brought closer to the glottis and there is less proximity of the food and air passages.   Because of the fact that the food is retained in the mouth and chewed, there is a high specialization of the glands, since some digestion is initiated in the mouth itself, before the food is swallowed.   The teeth are so patterned that they fit the type of food used.   (See Chapter III.)   The roof of the mouth, especially in the ungulates, is cross ridged and covered with well-developed horny spines.

Tongue. — A tongue of some kind is found in practically all vertebrates.   From its position in the mouth, it is probable that it was first used to assist in pushing food back into the pharynx.   In fishes the tongue generally is poorly developed, though in a lower group, the hagfishes (*Myxine*), it is covered with horny spines used to rasp away the flesh of fishes on which they live, and is moved by the musculature of the pharynx and innervated by the hypoglossal nerve.   Highly specialized tongues are not common in water-living animals, since their need for such a structure is not great; but in the land-living vertebrates the tongue assumes great importance, not only in handling food in the mouth, but also in procuring food.   The vertebrate tongue is generally tactile and may be supplied with taste buds.

Fishes have a primitive tongue structure, which is of little functional use.   It rests on the midline of the branchial skeleton on the floor of the mouth and extends from the hyoid to the branchial arch, the basibranchial being used as a support.

In amphibians the tongue varies greatly in size and importance. The Aglossa have none at all.   Frogs have a highly specialized structure which serves as a means of seizing food and drawing it into the mouth cavity.   In the Anura generally the tongue is attached at the anterior end of the jaw and is shot out with great rapidity, catching insects by means of its sticky covering.   The muscular system becomes better organized, with a genioglossus as a protractor and a hyoglossus as a

retractor, thus giving much more pliability. Its sense organs are in-nervated by the glossopharyngeal nerve, and its muscles by the hypo-glossal nerve.

The tongue in reptiles and birds has additional parts which make it more serviceable. The tuberculum impar a median, unpaired tubercle, which originates between the basihyal cartilage and the lower jaw, is added to the median part, and a fold is added to each side. In lizards and snakes the tongue is highly protractile and is often used for food-getting   A branch of the trigeminus serves these additional parts, so
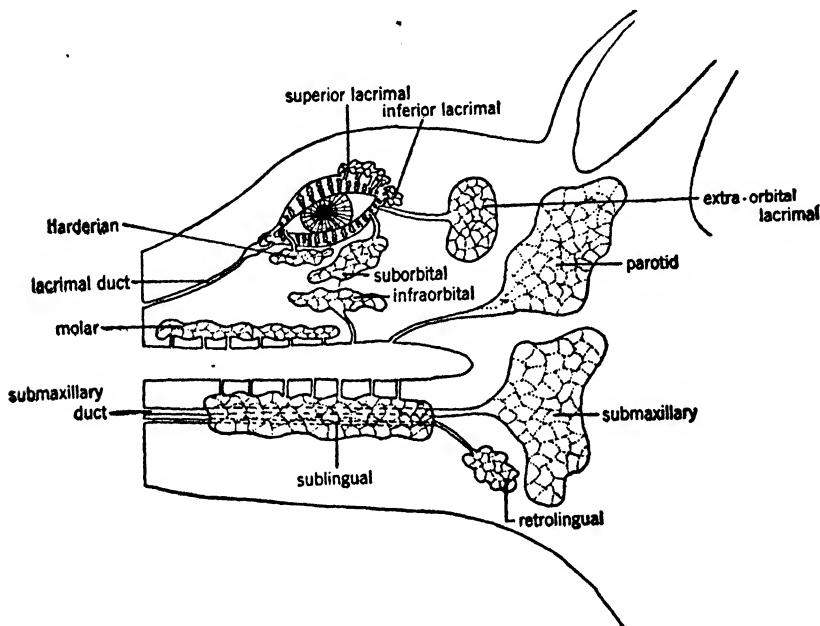
Fig. 138.   Diagrammatic arrangement of the salivary and lacrimal glands of mammal.   Redrawn from Plate and Weber.

that three cranial nerves are concerned in the innervation of the tongue. The skeletal parts consist of the modified visceral skeleton, which is used as a tongue support and generally consists of a median element and two cornua, or horns.   In woodpeckers the cornua are curved over the skull, ending at the nostrils, and are enclosed in a synovial sheath that permits free movement, so that the tongue can be protruded astonishingly far.

The highest type of the tongue appears in the mammals, where it is in constant use in grasping food, pulling it into the mouth, and moving the bolus, or ball of food, from side to side in mastication.   It also assists in swallowing and, of course, aids speech in man.   The skeletal parts

are somewhat reduced, with a median basihyal and a series of small hyals, *consisting of the cerato-, epi-, stylo-, and tympanohyal, the last attached* to the skull by a ligament. In man the stylohyal is ankylosed to the skull, forming a slender, sharp spike. This series is complete in the cat. (See Fig. 98 *C.*) Thyrohyals extend from the basihyals, forming the horseshoe-shaped bone at the anterior end of the larynx. The mammalian tongue seems to be a secondary structure superimposed upon another of older origin, although this may be disputed. The basal region, or sublingua, probably is the same as that of reptiles and birds; the fleshy region is peculiar to the mammals. This part of the tongue
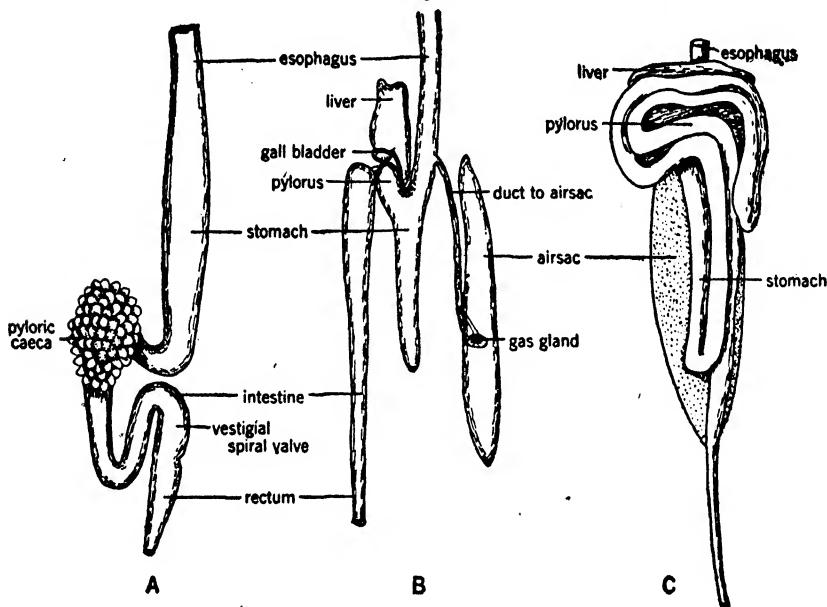
FIG. 139. Digestive systems of fishes. A, Lepisosteus; B, eel (Anguilla chrysypa); C, sucker (Catostoma commersoni).

consists largely of interlaced muscles, which make it capable of versatile movements. The tongue is supplied with a series of sensory structures principally concerned in taste and in touch. The taste buds are usually near the base of the tongue and around the circumvallate papillae. Each bud, or bulb, consists of taste cells, which are depressed below the surface and open by small orifices. They detect only materials in solution. Small papillae, shaped like small mushrooms, are scattered over the tongue in irregular areas. Carnovora and ungulates may have horny papillae which assist in holding and may be used in rasping. The tongue is richly supplied with blood vessels and lymph nodes. A

watery mucous secretion is supplied by other glands on the surface. Three nerves are concerned in the innervation, the trigeminus, glosso-pharyngeal, and vagus.

Glands of the Mouth. — The glands of the mouth are a development of land life, being absent in all but a few water forms. Their absence in water forms may be explained by the fact that the inflow of water with the food gives necessary lubrication but would dilute any glandular secretion and make it useless. Furthermore, food is held but momentarily in the mouth and commonly is swallowed whole. Animals that have returned to the water, such as turtles, water birds, cetaceans, and water mammals, have either lost the glands or have them greatly re-
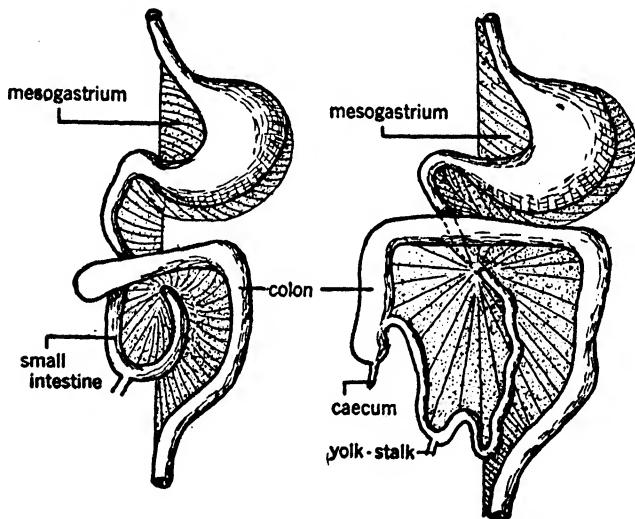
FIG. 140.   Development of mesenteries.   After Hertwig.

duced. The glands of the amphibians are few in number and are located on the roof of the mouth or on the tongue. Reptiles show a much greater development of the palatine, sublingual, premaxillary, and labial glands. The superior labials (Fig. 132) of the poisonous snakes and the lower labials of *Heloderma* produce venom. The mouth glands are generally little developed in birds, except at the corners of the mouth, but they reach their highest development in mammals where they supply three kinds of secretions: mucus, a relatively heavy lubricant; a serous fluid, a thin lubricant; and ptyalin, a digestive enzyme that acts upon starches. The labials, palatines, and buccals (modified labials) suggest the glands of the skin in their structure. The linguals, sublinguals, and retrolinguals, pour their secretions into

the mouth along the borders of the tongue (Fig. 138). The parotids, the largest mouth glands of the mammal, are ventral to the ear, at the angle of the jaw, and send their secretion into the mouth through the sides of the cheek by means of the parotid ducts. The submaxillaries are quite large and very much in evidence on the medial line of the throat, at the angle of the jaws. The submaxillary ducts (Wharton's) open under the tongue to the anterior part of the mouth. Ungulates have large molar glands that pour a copious supply of watery secretion over dry food. In cetaceans and sirenians, because of their long association with the water, the mouth glands are reduced almost to vestiges, but in the pinnipeds, since their water experience has not been so long, they are retained in their normal land condition.

Pharynx. — The pharynx, being concerned with respiration as well as digestion, exhibits more modifications than any other part of the digestive system. Its walls are broken through in the fishes by the gill slits, since the gill pouches finally gain openings to the outside of the body. These openings are universal in the fishes and retained in some of the amphibians. The posterior nares, originally opening into the anterior part of the mouth, become forced back to the pharynx by the formation of a hard palate in reptiles (Crocodilia), and this condition is typical of the mammals. The opening of the first gill slit is retained in all vertebrates above the fishes as the tuba auditiva, or Eustachian tube. In fishes the duct from the airsac generally opens into the pharynx (Fig. 139 B, C), though sometimes into the esophagus or even into the stomach. The lungs of land vertebrates open into the pharynx
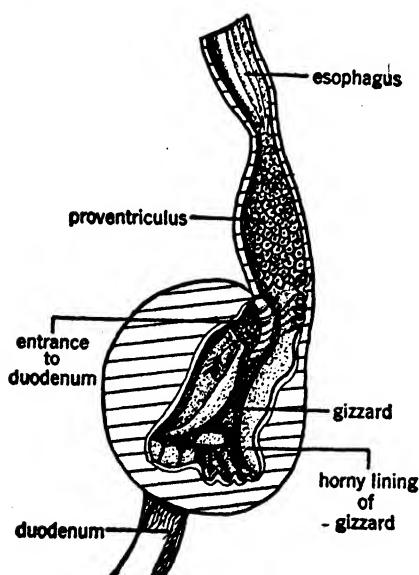
FIG. 141. Stomach of sparrow (Passer domesticus), sagittal section.

through the glottis, which has a protecting flap, the epiglottis, in mammals. The pharyngeal tonsils of the amphibians, reptiles, and birds are on the roof of the posterior choanae; the palatine tonsils, characteristic of mammals, are on the lateral side of the pharynx. From the floor originate a number of glands, including the thyroids, parathyroids, and thymus, all originally associated in development with the gill pouches.

Tonsils. — Several tonsil-like structures appear in the vertebrates. Fishes and amphibians have lymphoid glands in the pharyngeal region that, perhaps, have some relation to the tonsils of the higher vertebrates. Reptiles and birds have well-defined pharyngeal tonsils that also appear in some mammals. The lingual and palatine tonsils are characteristic of the mammals and are quite consistent in their appearance. The lingual tonsils are small, isolated, lymphatic structures that appear at the base of the tongue, consisting of a small pit, lymphatic nodules, and a small opening to the surface. They have the structure of a small palatine tonsil. The palatine tonsils are stable structures of the mammals and one of their characteristics. This tonsil originates from the pharyngeal region of the second gill pouch, starting as a small pit lined with mucous membrane that later forms simple folds. The folds may be complicated by the formation of a branching system for each fold. The tonsil is made up of a connective tissue capsule that partly surrounds it, folded mucous membranes with their lymphocytes and lymph nodules, adenoid tissue, and an opening to the throat. The tonsils of man have a rather complicated series of crypts and a single opening to the throat.

Esophagus. — The digestive tube proper starts with the esophagus, which is little modified, being simply a passageway through which the food reaches the stomach. In structure it resembles the rest of the digestive tube, in that it is surrounded by mucosa, submucosa, and muscular layers, but the serosa is lacking. Its function is to pass the bolus of food along to the stomach and supply enough glandular secretion for lubrication only, since the food ordinarily remains in it but a short time. Cyclostomes have little differentiation of the foregut, and it is rather difficult to draw a line between the stomach and the esophagus. Fishes also have little differentiation between the esophagus and the stomach, the principal difference lying in the glands and their distribution. A few fishes, as the eels and some of the elongated forms, have quite a clear distinction. The tube is often smooth, may be slightly folded, or may have horny papillae as in *Acanthias* and *Sturio*. Amphibia generally have a short undifferentiated esophagus, except in the elongated forms such as *Siren* and *Amphiuma*. The esophagus becomes much better differentiated from the stomach in reptiles, and may be lined with horny papillae as in turtles. Birds present some modifications partly because of the elongated necks found in this class. Two modifications occur, in one of which a crop is developed, for the storage of food, as in granivorous birds; in some of the meat-eaters, a dilated sac is used for brief food storage. Pigeons have a glandular secretion called "pigeon's milk" that is secreted and fed to nestlings. Mammals have a definite esophagus with a fairly close distinction between the esophagus

and the stomach, although in some cases the line of demarcation is not very clear. The rumen and reticulum, the first two compartments of the sheep stomach, are really a modified part of the esophagus (Fig. 143 *B*).

Stomach. — The stomach is a division of the digestive tube differentiated for food storage and the preliminary stages of digestion. It supplies digestive juices to the food and gets it in a proper condition for
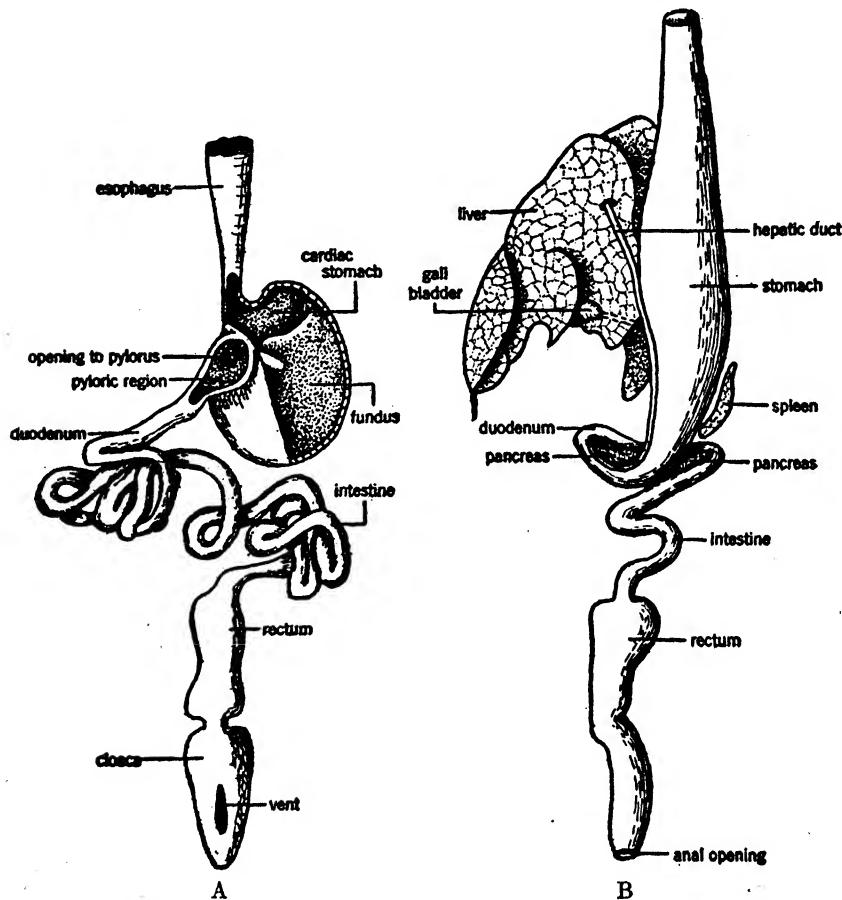
FIG. 142. Digestive systems of reptiles. A, alligator, B, Sceloporous.

action by the small intestine. It has a gentle motion that agitates the food and mixes it with the secretions of glands in its walls, which are incited to act by hormones or by the food itself. The stomach is held in place by the mesogaster (Fig. 140), a mesentery which suspends it from the posterior wall of the coelom. It is divided into several regions, each characterized by the presence of glands of a certain type: the

cardiac region, into which the food first goes, supplies an albuminous fluid; the fundus, or mid-region, supplies the gastric juice proper; the pylorus, or third region, adds mucus to the digesting materials (Fig. 144). The pyloric region is separated from the duodenum by a sphincter muscle,
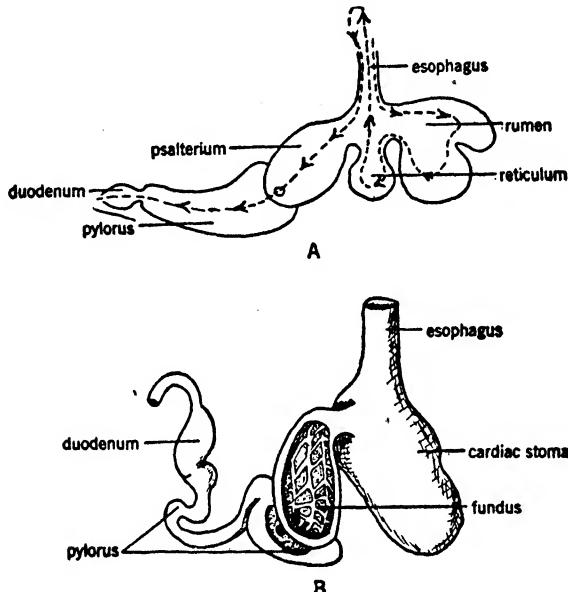
FIG. 143.   Mammalian stomachs.   A, the stomach of a ruminant showing the pathway of food through the divisions.   After Kingsley.   B, stomach of a seal. After Bütchli.
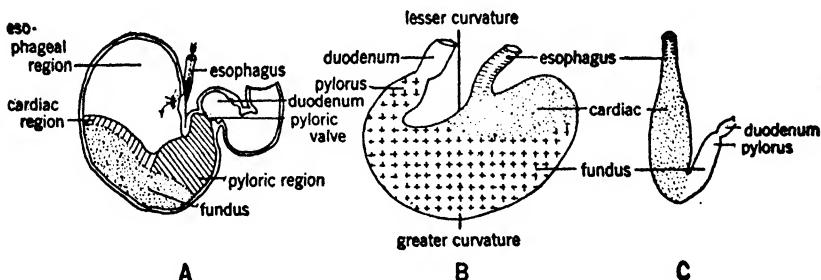
FIG. 144.   Mammalian stomachs.   A, stomach of horse.   After Sisson.   B, stomach of a rodent; C, stomach of a seal.   After Weber.

which permits small quantities of the stomach contents to pass when they are in a proper condition and have reached a definite stage of acidity.

The stomach in vertebrates generally is well supplied with blood vessels and lymphatics and is innervated by the autonomic system (coeliac plexus) and vagus nerve.   The mammalian stomach is variable

in shape, differing greatly in the various classes. Typically there is a greater curvature extending around the long side and a lesser curvature along the short side. The inside is folded so that the lining appears to be wrinkled. Besides the four layers of the esophagus, a fifth layer, the serosa, is added.

The simplest type of stomach is found in fishes and amphibians, in which it is little differentiated from the rest of the gut, but in higher forms it becomes much more highly specialized. More than a hundred caeca, centered around the pylorus (Fig. 139 A), are found in some fishes (bass). Many birds and reptiles have the habit of swallowing stones or other hard material to assist in grinding the food. The stomach of a grain-eating bird (Figs. 141, 142) is divided into two parts: a glandular region, or proventriculus, which supplies the juices; and a ventriculus, or gizzard, which is heavily muscled and lined with horny plates that assist in the process of reducing the food to a mash, thus compensating for the lack of teeth. In mammals the stomach usually consists of but a single chamber, but it may consist of as many as four in some ungulates. In sheep (Fig. 143 A), for example, the first two chambers (rumen and reticulum) are developments from the esophagus, and the last two chambers (psaltarium and abomasum) constitute the " true " stomach. The food, when partly chewed, passes down the esophagus into the large paunch, or rumen, which serves as a storage chamber. From this it goes into the reticulum, a small chamber with honeycombed walls, which rolls it into a ball, or cud, ready for regurgitation and mastication. On being swallowed the second time, it goes to the third chamber, the psaltarium, which mixes it with gastric juices, and thence to the fourth chamber, the abomasum, where the preliminary stages of digestion are continued until the food is in proper condition to pass through the pylorus and the duodenum into the small intestine. In one of the bats, a caecum is developed from the fundus, and in the hippopotamus a pair of caeca are developed from the same region.

Small Intestine. — The intestine, with its divisions, carries on the process of digestion and rejects the waste products as feces. Starting with a straight tube in lower vertebrates, it becomes lengthened, folded, and specialized, to have a large enough area for absorption, as the area must be in proportion to the bulk of the animal. The proportion is maintained by folding the inner surface, increasing the length, and developing spiral valves and side pouches, or caeca. The posterior limit of the duodenum is marked by the entrance of the ducts from the liver and pancreas. The duodenum supplies a hormone, secretin, which enters the blood and causes the pancreas to release its juices. The small intestine receives the food material from the duodenum, and here

the process of digestion is completed by the addition of the succus entericus, or intestinal juice, and absorption takes place. In the mammal, the small intestine is divided into two regions, the jejunum and ileum.

The lining of the small intestine is thrown into concentric folds or ridges, called plicae circulares, by thickenings of the mucosa and submucosa, and on these ridges are placed the villi, small finger-like processes that select and absorb the digested food. The villi cover the surface of the small intestine, giving it a soft, velvet-like appearance. Each villus is made up of a small artery and vein, a nerve, and lymph vessels. The glands of Lieberkühn, which supply the succus entericus, have their openings at the bases of the villi. The small intestine is
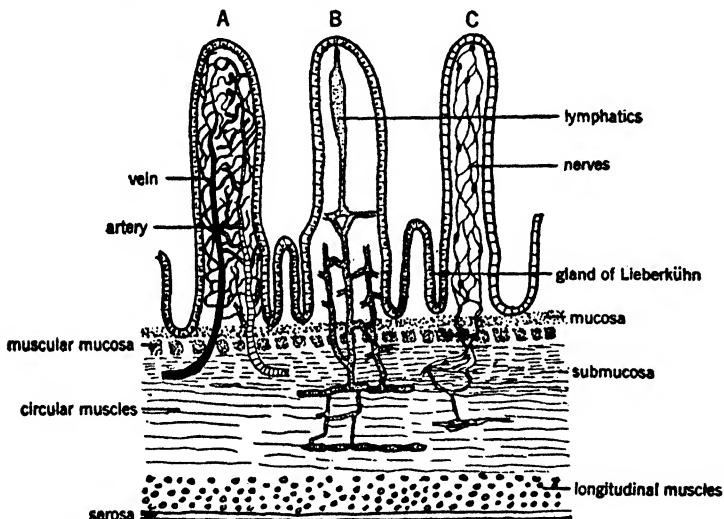
Fig. 145. Diagrammatic drawing of the villi of the intestine. A, blood vessels of the villus; B, chyle vessels; C, nerve net. Modified from Mall.

richly supplied with blood vessels, because it is here that the process of absorption is carried on. Food enters the blood stream through these villi, being taken into the veins and thence through the connecting vessels to the hepatic portal and the liver. Fats are absorbed by the lymphatic system of the villi, and going through the lacteals of the mesenteries, reach the venous system, anterior to the heart, through the thoracic ducts. (Fig. 145.)

Lymph vessels and structures are associated with all digestive tubes, but they become prominent in the reptiles and continue through to the mammals, where they form large aggregates in the walls of the digestive system. They may be simple follicles scattered along the tube, or they may be collected into aggregates or patches, as in the mammals, where

they form the Peyer's patches. These patches of follicles are most plentiful in the small intestine, although they may extend into the colon. In the human intestine these patches may be half an inch wide and three or four inches long. They occur on the wall of the intestine, opposite to the attachment of the mesenteries. They appear as raised areas and are quite distinct. Prominent in young animals, they become less conspicuous with age. In typhoid fever, these patches are broken down by the action of the bacteria so that the intestinal wall is perforated.

Caeca (Fig. 309), which may occur at the junction of the small and large intestines, are additional storage and digestive regions. These may be very large in reptiles, birds, and some mammals, but in the primates they are reduced to small vestigial structures, such as the vermiform appendix of man, which appears to have little or no function. The rhythmic action of the longitudinal and circular muscles, which are controlled by the autonomic system, causes a gentle peristaltic movement that advances the food slowly through the entire digestive tube (Figs. 139, 142, 147).

The lower end of the intestine may have a spiral valve (Fig. 146), or it may be enlarged to form a colon as in the higher vertebrates. In mammals the junction is quite abrupt, often at right angles, and usually marked by the caeca either paired or single. Most of the absorption has taken place by the time the food reaches the large intestine, and this distal end of the digestive tube is used to reduce the bulk of the feces by extracting the water. In animals eating large amounts of cellulose, some reduction and digestion may take place, usually by bacterial action. The villi generally disappear at the beginning of the large intestine, or at most extend but a short distance along its length. Its
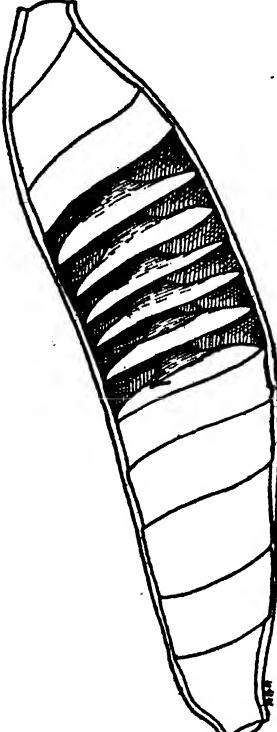
FIG. 146. The ileum or spiral valve of the shark, Squalus acanthias.

surface is not so much folded, and the plicae circulares disappear. Lymph nodules are found in the tube, but no structures resembling Peyer's patches. Its juices are supplied by mucous glands, whose general function is to supply lubrication.

The rectum (Figs. 142, 147), is a relatively short, thick-walled region at the distal end of the colon, concerned in the expulsion of the feces.

The anus, or outlet, is protected by sphincter muscles, which in the higher animals are innervated by both the autonomic and voluntary systems.

The vertebrates generally, except the placental mammals, have a common outlet for the digestive and urogenital systems, which is called the cloaca (Figs. 288, 298, 309). In vertebrates below the mammals the cloaca may have pouches for the storage of urine.

The Liver. — The liver is the largest gland of the body; originally it was on the walls of the intestine, but it has pulled away and now is
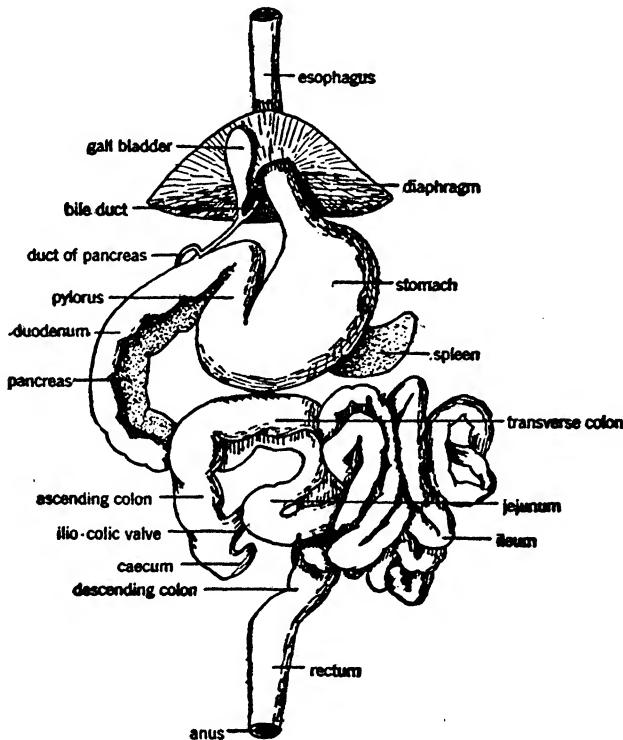
FIG. 147. Digestive system of the cat (liver removed). After Davidson.

connected only by ducts. In structure it is a tubular gland that has masked its appearance by overgrowth. In ancient days it was regarded merely as packing for the rest of the organs, but now it is recognized as important, not only in digestion, but also in the chemistry of the blood.

The shape of the liver varies with the body of the animal, being short or long according to the body form. It is generally divided into two unequal parts, each with a varying number of lobes (Figs. 148, 298). It is covered with a part of the serosa, which follows it in its develop-

ment. It is attached by the coronary ligament to the diaphragm, by the falciform ligament to the ventral body wall, and by the gastro-hepatic ligament to the stomach. The texture of the liver is such that it is easily ruptured, since it has little connective tissue in its structure and its serosa offers only a slight protection. The unit of structure is the type usually found in a tubular gland, each unit consisting of polyg-onal cells which form a liver lobule.

The tissue of the liver (Fig. 149) itself is supplied by the hepatic artery. The venous blood from the digestive tube is carried to the liver by the hepatic-portal vein, which delivers it to the capillaries of the individual lobules, where it is exposed to the action of the cells of the lobule. Along these capillaries are the fine, interlacing bile ducts which collect the bile and carry it to the hepatic duct and to the gall bladder if one is present. The common bile duct, or choledochal duct, carries the bile from the hepatic and cystic ducts to the intestine, discharging
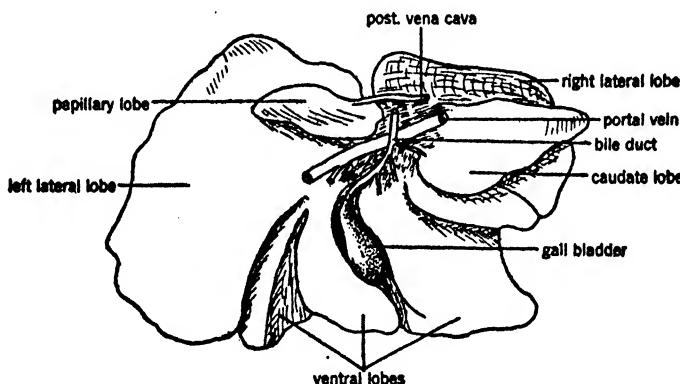
FIG. 148. Liver of the dog. After Sisson.

it through the influence either of a hormone or of the fats in the food. The liver is innervated by branches from the vagus nerve and also from the coeliac plexus of the autonomic system.

Besides supplying the bile for the digestion of fats, and for lubrica-tion, the liver stores glycogen, a simple sugar, and as a ductless gland it introduces into the blood stream an enzyme that is used in the di-gestion of nitrogenous and carbohydrate materials. Urea and uric acid, formed in the liver from the ammonia compounds of the blood, are sent to the kidneys for removal. Old and worn-out erythrocytes are also removed from the blood stream by the liver.

Pancreas. — The pancreas, a companion gland to the liver, is a mar-velous chemical laboratory in a small space and one of the most impor-tant glands of the body. It takes its origin, as does the liver, from the

walls of the digestive tube, and is a constant structure in all vertebrates. Originating from three diverticula, it becomes consolidated to form one gland with several ducts, usually a main pancreatic duct (duct of Wirsung) and an accessory duct (duct of Santorini), although more ducts may be present in lower forms. Frequently the ducts join those of the liver and enter the duodenum through a common duct. Its position is always close to the intestine, and it often follows a fold so that it becomes a U-shaped organ. Its structure is that of an acinose gland. The pancreatic juice, incited to flow by the secretin from the duodenum, which reaches it through the blood stream, supplies all the enzymes necessary to complete the digestive processes. Its removal causes death to the animal. The islets of Langerhans, in the tissue of the pancreas, supply a hormone that is very essential in the control of the amount of sugar in the blood. This hormone, isolated by Banting and Best in 1921, was named insulin and is now used all over the world for the control of diabetes (Figs. 147, 298).

The digestive system, though performing some of the most complicated chemical processes, undergoes no radical changes from the lowest to the highest vertebrates. As the requirements of digestion are much the

FIG. 149. Section of liver. After Weber.

same in all vertebrates, as far as the main features are concerned, the greatest variations and improvements come in meeting the conditions imposed by different foods, and in maintaining the area of the digestive tube in proper proportion to the bulk of the body.

Résumé

Digestion is the process of simplifying food materials and preparing them for absorption by the cells of the body. The digestive tube is formed early in embryonic development and is lined with endoderm, except for the mouth and rectum, which have ectodermal linings. Digestion starts in the mouth and is continued in the stomach and small intestine, most of the absorption occurring in the small intestine and only a slight amount in the stomach and colon. All digested foods except fats are taken into the blood stream and thence to the liver before entering the heart. The mouth of chordates is a new structure,

not to be compared with the mouth of invertebrates. The tongue is relatively unimportant in fishes, but in tetrapods it becomes very important, with varied uses, and has tactile and taste buds. The tongue is held in position by the hyoid arch. Mouth glands, insignificant in fishes, assume importance in the tetrapods. The principal glands are the paired labials, palatines, buccals, linguals, sublinguals, maxillaries, submaxillaries, and parotids. The pharynx is modified by respiratory functions. The esophagus is usually a simple tube, supplied with lubricating glands. The stomach, which usually consists of cardiac, fundus, and pyloric regions, may be divided into four compartments in ungulates. The duodenum is a short section of the small intestine, limited anteriorly by the pyloric sphincter and posteriorly by the duodenal-jejunal flexure. The small intestine supplies digestive juices, and through the villi of its walls the greater part of absorption takes place. The villi contain blood vessels, lymph vessels, and nerves. The layers of the intestine are the inner mucosa, the submucosa, the circular and longitudinal muscles, and the serosa. The large intestine, which has few or no villi, reduces the feces by extracting water but absorbs little or no food. The rectum is a short, thick-walled region at the distal end of the colon. The liver, a tubular gland, originating as a diverticulum from the digestive tube, stores glycogen, extracts waste from the blood, and secretes bile, which goes to the distal end of the duodenum through the choledochal duct. The pancreas, also originating as a diverticulum from the digestive tube, secretes the pancreatic fluid, which digests all foods and supplies a hormone, insulin, from the islets of Langerhans.

CHAPTER VII

CIRCULATORY SYSTEM

Since many parts of the vertebrate body are deeply buried, and since the skin is not able to carry on all the work of respiration, early in invertebrate history some circulating medium was necessary to solve the problem of the distribution of materials, together with the carrying of food, the removal of waste, and other complex functions connected with hormones, enzymes, and immunity to disease. These needs were met by the circulation of the blood.

The plasma is a straw-colored fluid containing: water; food; waste; salts; enzymes; products of the ductless glands, or hormones; materials concerned with immunity and toleration of disease germs, toxins, and antitoxins. The plasma also contains fibrinogen, a substance which forms threads and thus assists in the formation of clots when the blood is exposed to air or to foreign structures or materials. Clotting is further aided in mammals by the small platelets which disintegrate rapidly in exposed blood.

The red corpuscles, or erythrocytes, found in all vertebrates, are small cells, concerned principally in the carrying of oxygen to the tissues. They contain haemoglobin, which has the power to take up large quantities of oxygen, and in this way it is carried to the different parts of the body and released. Erythrocytes are used up in a short time, so a continuous supply is being made in the red marrow of the long bones. The erythrocytes of the lower vertebrates are large with a very distinct nucleus; the mammals are unique in having no nuclei in mature corpuscles. The erythrocytes never leave the arteries, veins, and capillaries.

The leucocytes, or white corpuscles, are ameboid in shape and are larger than the red. They are able to leave the veins and arteries through the walls of the capillaries and get into the tissues and the lymph stream. They have the ability to move with an ameboid movement. They are differentiated into several types with quite different functions. They carry materials from place to place in the body, remove dead cells, combat bacteria and other parasites that find their way into the blood stream, and act as guardians of the circulatory system generally. New leucocytes are formed in the lymphoid tissues and added to the system.

The functions of the blood are numerous and complicated. The food supply from the digestive tract is carried to the cells by the blood;

water and oxygen are carried to the tissues and liberated; and hormones and enzymes are carried to the place where they are needed. The removal of waste is accomplished as the blood circulates around the body.
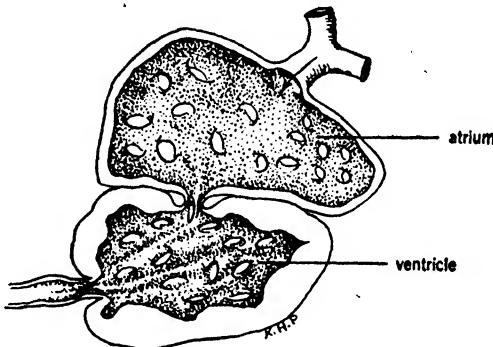
FIG. 150.   Section of heart of *Ichthyomyzon concolor*, Silvery lamprey.

Waste materials are taken into the stream to be disposed of at special points, and carbon dioxide is collected and taken to the lungs where it is removed. The lungs enable the blood to get a new charge of oxygen
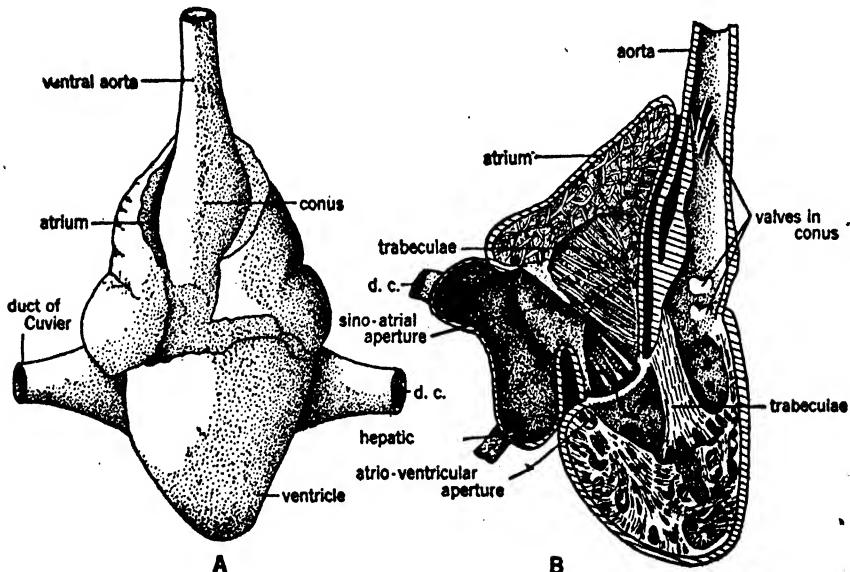
FIG. 151.   Heart of Amia.   A, anterior; B, sagittal section.

after discharging the carbon dioxide. Nitrogenous and other wastes are removed by the kidneys, and the skin removes some surplus water and salts. The liver removes worn-out erythrocytes and stores surplus

materials not needed at the time, and many parts of the body are used to store surplus fats. The regulation of temperature is one of the important functions, and in this the circulatory system is linked with the autonomic, which regulates the supply of blood to outer or inner tissues.

The circulatory system consists of the heart, which is a central force-pump; the veins, which carry blood to the heart; the arteries, which take it away; and the capillaries, which connect the arterial and venous systems. The veins are thin-walled and have pocket valves at intervals; the arteries have much thicker and stronger walls. Muscle tissues and their connections with the autonomic system make possible the dilation and constriction of both systems. The lymphatic system is an important link in the circulation, since it returns the plasma that has escaped from the vessels into the tissues. (Fig. 274.)

The circulation problem is one that concerns all living tnings, since there must be ways for transporting materials to and from all parts of the living structure. This transportation is rather simple in the lower animals, but it becomes very complex with higher organization and with types of covering that are more impervious and prevent an interchange of gases. As these coverings develop, definite areas are established for oxygenation, taking away waste, and adding food materials, and other problems associated with the circulating medium are solved. Definite, closed systems do not usually occur below the vertebrates, since the lower animals have less definite vessels, with lacunae or open spaces in which the circulating fluid can collect.

The blood systems of the lower acraniates are of the invertebrate type; the cephalochordates approach the vertebrate type. *Branchiostoma* (*Amphioxus*) has a fairly well-defined blood system in which the vessels are well established, with dorsal and ventral vessels, a regular flow of the circulating fluids, and a propelling heart. The blood is aerated in the pharyngeal chamber, and all the blood passes through the capillaries of a hepatic system before going to the heart and through the rest of the circuit. The heart is a valveless, single-chambered structure that directs the blood forward, principally because of mechanical features that prevent forcing it back through the liver capillaries. The blood itself is colorless. The cyclostomes, or lowest living vertebrates, have a well-established circulatory system that is both primitive and specialized. The heart has two chambers (Fig. 150), an atrium and ventricle, both with a pair of valves. A small bulbus is present at the beginning of the ventral aorta. The specialization is noticed in the loss of the left Cuvierian duct in *Petromyzon*. The blood of the cyclostomes is red and has both types of corpuscles.

The Heart

Since the greatest possible freedom of movement is needed for the heart, it is enclosed in a special pericardial cavity, surrounded by a pericardial sac, and immersed in a serous fluid which supplies the necessary lubrication. The epicardium, a smooth layer of mesodermic tissue, covers the heart, and the endocardium lines it.

The heart makes its appearance in the lowest chordates, where it is one-chambered, but in the fishes it is two-chambered, being divided into a muscular sac, the atrium, and a heavier muscular chamber, the ventricle. It is three-chambered in amphibians and four-chambered in birds and mammals. It is equipped with valves, so that the blood once.started through cannot return to the chamber from which it was forced.
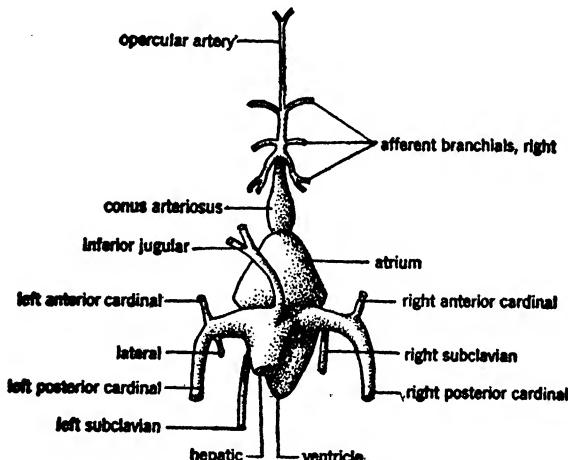
Fig. 152. Heart of Lepisosteus, posterior. After Schimkewitsch.

The relation of the heart to the head region undergoes a continuous change from fishes to mammals (Figs. 288, 298). In fishes and amphibians, the heart is immediately posterior to the head and in close connection with the gills, which naturally have a decided influence on its position. There is a slight retraction in the amphibians, but the heart is still well forward. In amniotes, however, there is a gradual shift to the posterior with the development of the lungs and the elongation of the neck, so that the heart takes its place in the body cavity and carries with it the elongated blood vessels of the carotid and jugular system.

Heart of Fishes. — The two-chambered heart of the fishes has the rather simple duty of pushing the blood from the body through the gills, with no return to the heart itself until the circuit is completed. The

position of the heart is just posterior to the visceral arches and very close to the gills, as it should be. But two chambers are necessary for this operation, and the heart of a fish consists of a thin-walled accessory chamber, the sinus venosus, which collects the returning blood from the ducts of Cuvier and the hepatic veins, and delivers it to the thin-walled atrium. A thin membraneous partition makes a partial separation of the sinus and the atrium. The passage of the blood from the atrium to the ventricle is almost mechanical, since the atrium is directly over the ventricle, so that a gentle pressure drops it into the ventricular chamber.
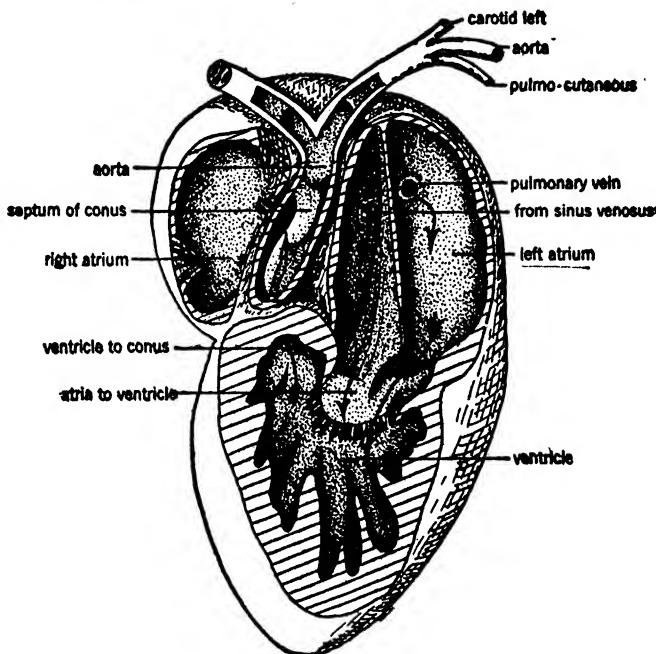
FIG. 153. Heart of frog dissected to show interior structures. After Kerr.

A pair of flaps serves as a valve between these two chambers. As the blood leaves the heart and enters the aorta, another series of valves prevent the return of the blood to the heart, since the conus is rather heavy walled with pocket valves which hold the blood until it can get through the efferent vessels and reach the gills. The expansion of the aorta at its base, forming either a conus or a bulbus, keeps the pressure on the capillaries of the gills constant. There is a reduction of the conus and valves in the teleosts, where only one set of valves is present (Figs. 151 *B*, 152, 275, 276).

The most notable change in the heart of fishes occurs in the lung-

fishes, where a new circuit is introduced by the return of the blood from the airsacs to the heart. The heart responds by starting the formation of a division of the atrium, so that there is a small, partially separated left atrium for the reception of the blood from the airsac. In the distribution of the blood from the heart, a condition similar to that of the amphibians is set up, in that the blood from the airsacs is directed to the body rather than to the gills. The lung-fish condition approaches quite closely that of the urodeles, the lowest of the tetrapods. A comparison of the hearts of urodeles and lung-fishes at first suggests some relationship, but probably convergence is the proper explanation, since both use the heart in the same way and have the same mechanical problems. The lung-fish heart is striking in at least two particulars: first, because of the fact that the blood from the air-bladder returns to the left side of the atrium; and second, because of the development of a partial septum between the two sides of the atrium. The conus has a spiral twist, and the distribution of the blood is similar to that of the urodeles in that the best blood goes to the body while the poorest returns to the air-bladder and gills.

Heart of Amphibians. — (Figs. 153, 288, 289.) The lung system of the amphibians is a lung-gill-cutaneous system, since all three of these may influence the blood. The amphibian heart continues changes that were suggested in the adaptations of the lung-fishes to air breathing. With lungs as a means of aerating the blood, and a return of this blood to the heart, the heart became three-chambered by the division of the single atrium into a right and a left half, the left receiving the blood from the lungs and the right the blood from the body and the cutaneous system. Within the Amphibia, there is considerable variation because of the different life histories. \The lungless salamanders, generally living in swift streams, have lost both trachea and lungs, as well as the septum dividing the atrium. These lungless animals must depend entirely upon the cutaneous system and the highly developed buccal-pharyngeal region, where the capillaries act as in the lungs. The urodeles that retain gills throughout life, as *Siren,* and *Necturus,* have poorly developed lungs that are little more than sacs, but the heart has paired atria and there is a slight separation of the different bloods, although the influence of the lungs is small. The conus is simple in these urodeles, and the spiral fold is lacking. It really makes very little difference where the blood goes after it reaches the conus. Urodeles that lose their gills have a much better lung, for they must depend upon the lung and the cutaneous system for aeration. These urodeles that go to land and lose their gills develop a spiral fold and valves, so that the blood is directed into a lung-cutaneous stream and a systemic stream for the body.\

The toads and frogs have the highest type of heart, since the ventricles have numerous trabeculae, which partially separate it, while a spiral valve and several pocket valves make a very good separation of the blood into a lung-cutaneous and a systemic stream (Fig. 153). The sinus venosus is reduced and becomes a part of the right atrium. Although the separation of the blood is through numerous trabeculae, the delivery to proper channels is surprisingly accurate, the blood from the lungs going to the body and that of the body to the lungs. The amphibian heart is folded in an S shape so that the atria are dorsal to the ventricle and in a more favorable position to deliver the blood into the ventricle through the atrio-ventricular valve. From the position of the right and left atria, the blood, when dropped into the ventricle, is for the instant unmixed, the blood from the right atrium being nearest
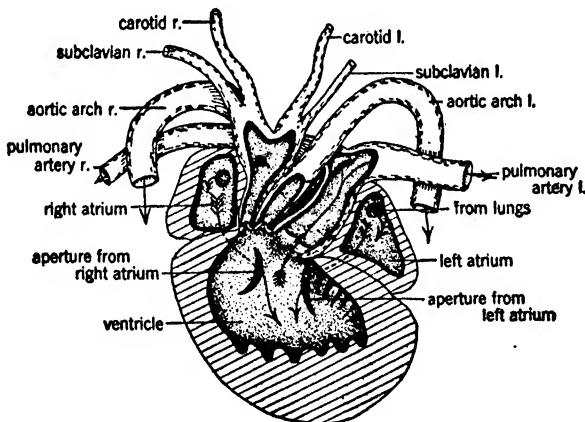
FIG. 154. Heart of turtle (Chelydra), dissected to show internal structure.

to the conus while that from the left atrium is at the posterior region of the ventricular chamber. In systole, the venous blood enters the conus and is guided by the spiral flap into easy channels, through the sixth arterial arches to the lungs. With these filled, the remaining blood is forced through the other arches to supply the body. The cutaneous system acts as an accessory, to enrich the blood supply. The blood of amphibians is never pure, except in the pulmonary veins, but there is a fair separation of the venous and arterial bloods, primarily through mechanical specializations of the heart rather than because of separate blood channels.

Reptilian Heart.—(Figs. 154, 155, 298, 301.) The heart of the amniotes is changed to fit a system in which the entire aeration of the blood is through the lungs. This has had a decided influence on the heart, and a number of structural changes occur that mark the difference between

-the heart of the amphibian and the reptile. The interatrial septum is complete, and there is an extension of the septum into the ventrical so that it is partly divided. The sinus venosus loses its significance, joins closely to the right atrium, and is no longer a separate structure. The aorta is split nearer the base, so that the pulmonary arteries are practically separate and there is little intermixture of blood at this point. The aorta thus splits into three main channels — the pulmonary, systemic, and the carotid blood streams — each protected at its outlet by a pocket valve. The continuation of the septum down into the ventricle makes changes in the valves necessary, and the reptiles have much better valves. From the mechanical standpoint, the reptilian
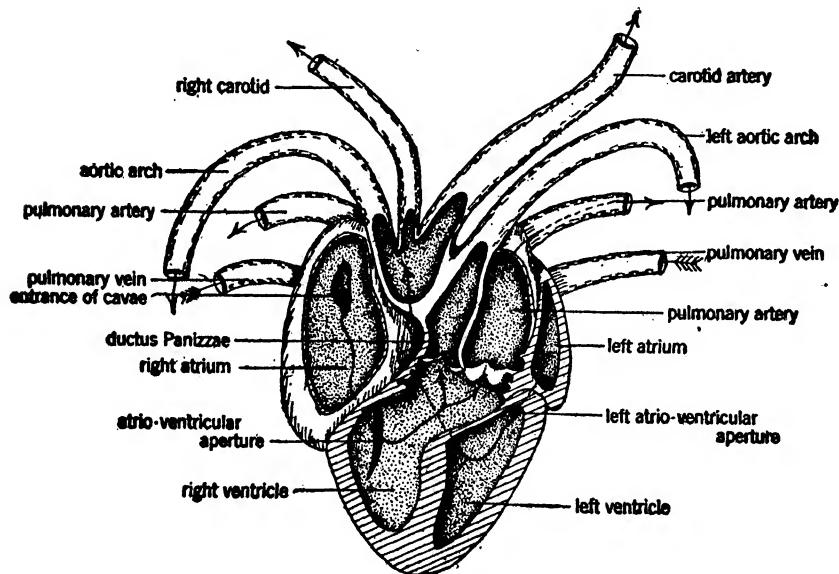
FIG. 155. Heart of alligator, dissected to show internal structure.

heart is rapidly approaching the perfection found in the birds and mammals. Crocodilia have a complete separation of the ventricles, into a right and a left, and it is not unreasonable to suppose that some of the other Reptilia, such as the dinosaurs and pterodactyls, also had a complete separation of the blood and four-chambered hearts. There is a small opening at the base of the aorta, the ductus Panizzae (Fig. 155), that does permit of some leakage, but it is rather small.

Hearts of Birds. — (Fig. 311.) The bird heart is divided into four perfectly separated chambers, and there is no intermingling of the blood at any point. All the defects of the reptilian heart are remedied, since the bird, with its very active life, would fare poorly with any mixture of

arterial and venous blood. There is a further reduction of the sinus venosus, which is practically obliterated. The right ventricle remains a thin-walled chamber that partly encircles the left. The left ventricle is heavy-walled, since it must force the arterial blood all over the body. There is a complete division of the aorta so that there is no ductus Panizzae as in the four-chambered reptile hearts. The atrio-ventricular valve is completely divided by a septum formed by the fusion of the endocardial cushions which function as dorsal and ventral valves in the Amphibia. Though highly specialized, it is still a modified reptilian heart.
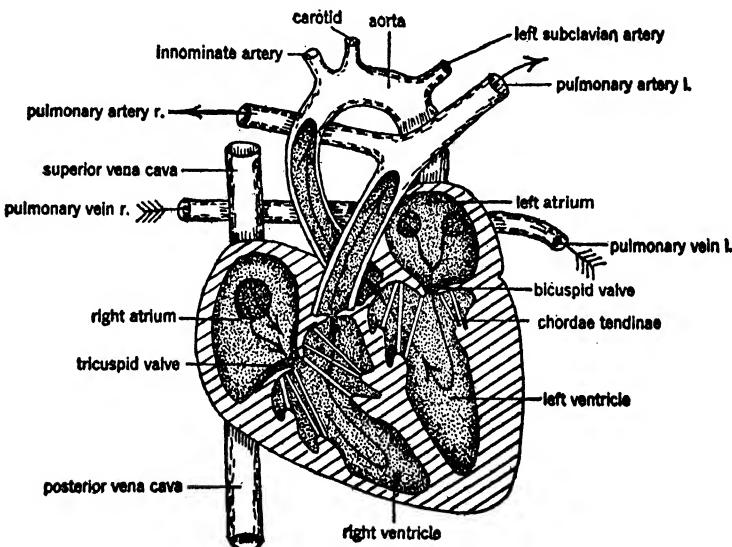
FIG. 156. Diagram of mammalian heart. Modified from Pearse and McLeod.

Heart of Mammals. — (Figs. 156, 157, 158, 159.) Mammals as well as birds achieved a four-chambered heart, but coming from different lines of reptilian ancestry, they did it in different ways. The heart of the mammal is equal to that of the bird in efficiency, and is the same double pump, with a complete separation of the blood at all times. The blood, brought in from the head region through the superior cavae and from the posterior region through the posterior cava, enters the light-walled right atrium, where it is held until it is sent to the right ventricle. The atria are quite distensible and are able to handle any extraordinary rush of blood. From the right atrium, the blood is sent through the tricuspid valve to the more muscular right ventricle, which sends it to the lungs for the exchange of gases. Since this is a light task, the walls of the ventricle are comparatively thin in contrast to the heavy

left ventricle. Semilunar valves prevent the backflow of the blood from the pulmonary arteries. The left atrium, which receives blood from the lungs, is also rather light-walled and capable of distension. The blood from the lungs may come through one or more openings. Forced from the left atrium, the blood goes through the bicuspid valve (mitral) to the left ventricle. The left ventricle is heavy-walled, since it must force the blood over the entire system. Its bicuspid valves are very heavy, and the chordae tendinae and papillary muscles are suffi-
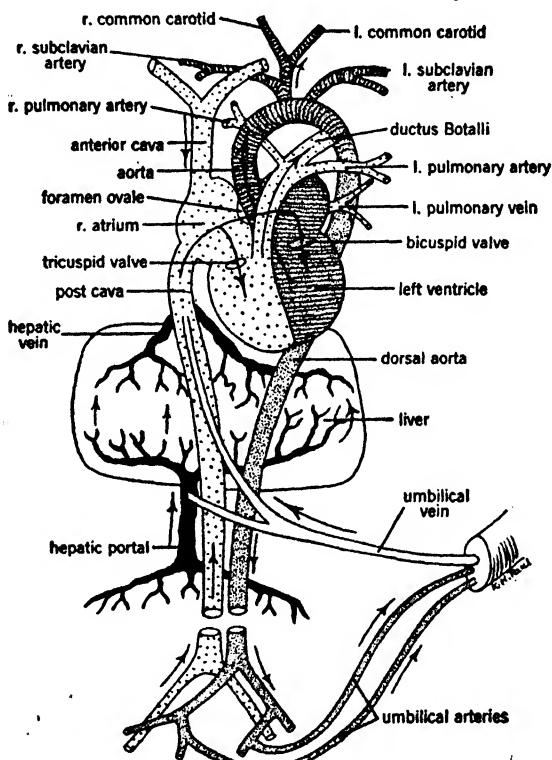
Fig. 157. Embryonic circulation of a mammal. After Weber.

ciently strong to prevent the forcing back of the cusps (Fig. 158). The outlet through the aorta is protected by semilunar valves, which prevent any backflow from the aorta during diastole.

In embryos of mammals (Fig. 157), a foramen ovale forms a connection between the atria, and some of the blood may go through this channel and thus avoid going needlessly to the lungs. Recent investigations seem to show, however, that this valve is too small to permit much blood to go through. A short time after birth, or at the end of a few

days, this foramen becomes more or less obliterated by a fold of muscle from the septum. In adult animals, it is often large enough to admit a small probe, but it is protected by the septal valve, and probably no blood can go through. Some human cases have been observed in which this foramen was large (ten millimeters) and remained open throughout life.

COMPARATIVE TABLE OF HEARTS

Fishes	Amphibians	Reptiles	Birds	Mammals
Ductus Cuvieri (Common cardinals)	Retained in some, modified in others	Part taken into atrium .	Part taken into atrium	Part taken into atrium, rest forms pre-cava
Sinus venosus	Being taken into atrium	Entirely in right atrium		
Atrium (1)	Atria (2) Division complete	Atria (2) Division complete	Atria (2)	Atria (2)
Ventricle (1)	Ventricle (1)	Ventricle partially divided	Ventricles (2)	Ventricles (2)
Conus with valves	Conus not divided	Conus divided	Conus division complete	Conus gone

The valves of the mammalian heart are simple but very efficient, consisting of cusps of tissue anchored by heavy chordae tendinae, which are attached to the walls of the ventricles by papillary muscles, thus preventing any possibility of their being pushed through *in systole*, when the blood is forced out of the ventricles. The heart beat consists of, first, the contraction of the atria, and second, the contraction of the ventricles; and the contraction is paired, first the two atria followed immediately by the two ventricles in the four-chambered heart. The heart beat is initiated by the atrio-ventricular nodes and distributed by the atrio-ventricular bundle (Fig. 159) or the bundle of His. This neuromuscular bundle extends down the septum between the atria and ventricles and spreads over the heart, sending branches to the different regions. This bundle synchronizes the heart beat. Vessels leaving the heart are provided with semilunar valves to prevent backflow of blood. Both the aorta and pulmonary arteries have these protecting valves. Incoming vessels of the right atrium are also provided with valves, consisting of folds of the endocardium that are somewhat rudimentary. The Eustachian valve is a slight endocardial fold along the posterior border of the inferior vena cava. The valve of Thebesius protects the entrance of the coronary sinus as it enters the atrium. The innervation of the heart is through the vagus nerve (X), which acts as a depressor, and the autonomic, which acts as an accelerator. Although supplied with

nerves, the heart seems to be somewhat independent of them, for even
if all the nerves are cut away, the heart tissue will continue to beat for
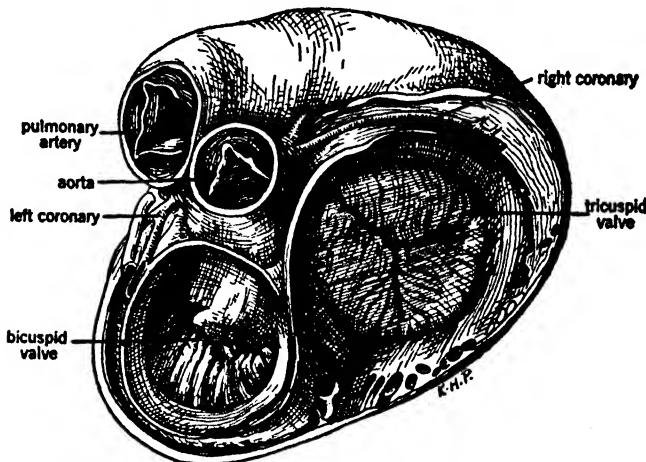
FIG. 158.   Cross section of the human heart, between the atria and the ventricles, to
'show the atrio-ventricular valves.   After Toldt, Hochstetter.
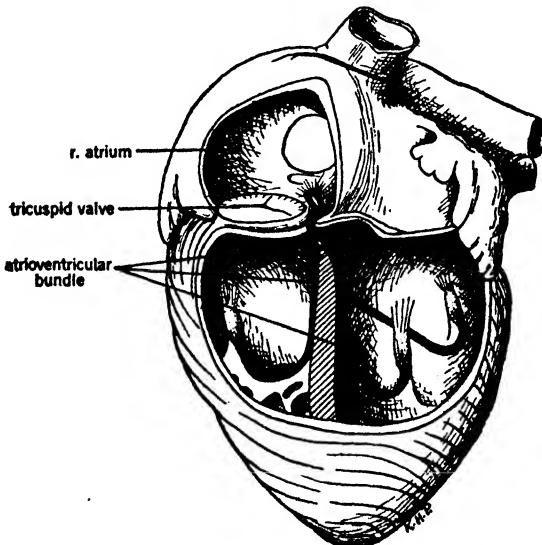
FIG. 159.   Mammalian heart to show atrio-ventricular bundle or bundle of His.
After Bolk, Göppert, Kallius, Lubosch.

a long time, even for years, under the proper conditions.   The heart is
enclosed in a pericardial sac, filled with a serous fluid in which the heart
beats with a minimum of friction.   The pericardial sac is held in place

by the large vessel entering at the anterior end and the attachment to the diaphragm at the posterior end. The blood supply of the heart comes through the coronary system, vessels arising from the aorta just after it leaves the heart. The coronary veins receive the blood from the capillaries and return it to the right atrium, through the coronary sinus. The lymphatic system is well distributed over the entire heart.

The Aortic Arches

The aortic arches consist of afferent and efferent vessels, interrupted by the capillaries of the gill lamellæ in fishes and in Amphibia by the type peculiar to this group. These vessels connect the heart with the
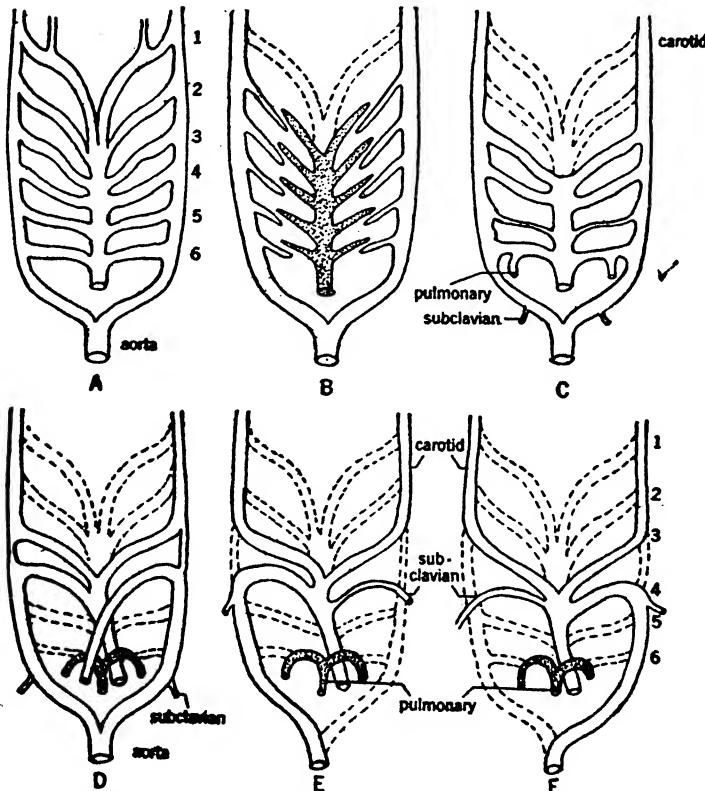
FIG. 160. Diagram of aortic arches, ventral view. A, primitive; B, shark; C, urodele; D, reptile; E, bird; F, mammal.

dorsal aorta, through which the arterial blood is directed to the different parts of the body. The arterial arches lie on the outside of the gill bars or visceral arches. Because of their persistence in the developmental
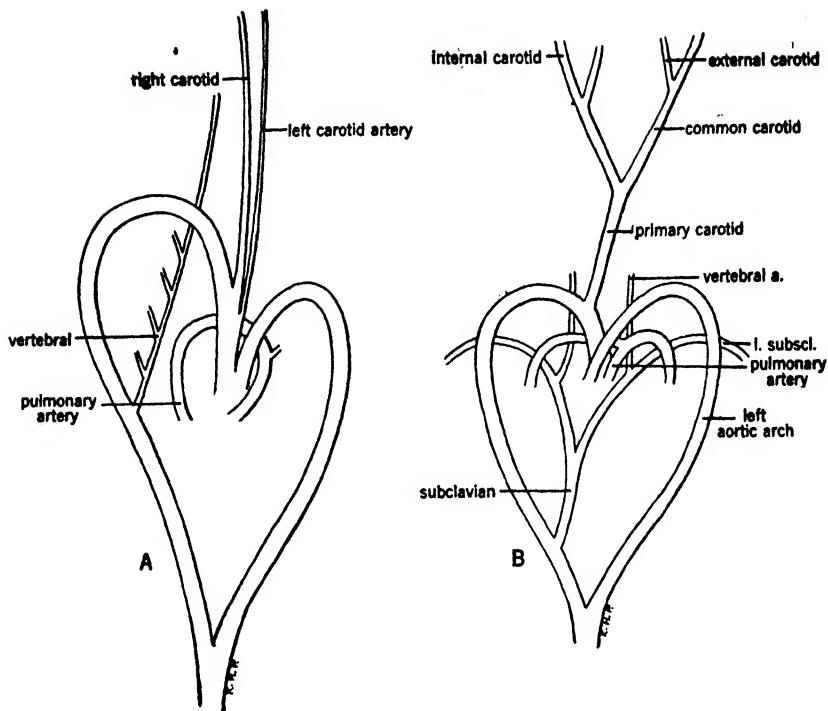
FIG. 161. Aortic arches. A, Boa; B, Varanus, a lizard. After Hafferl.
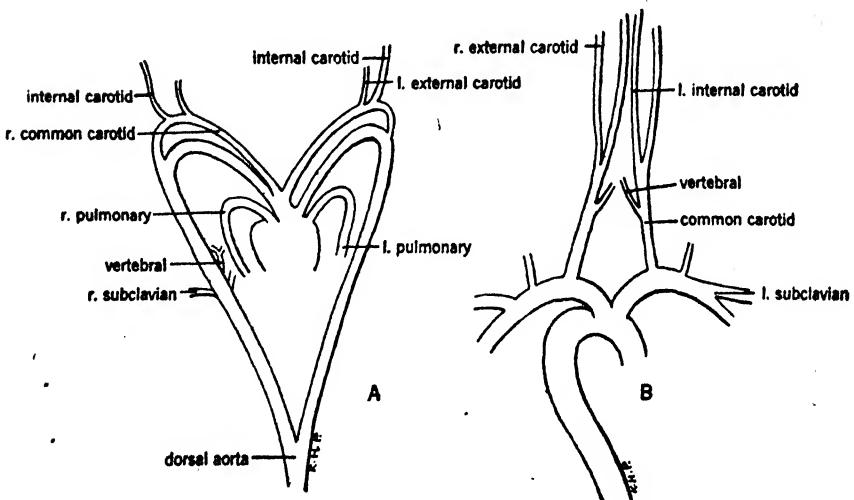
FIG. 162. Aortic arches. A, lizard (Lacerta); B, bird (goose). After Hafferl.

stages of all vertebrates, they are of great interest to embryologists and to anatomists (Fig. 160). The primitive arch system consists of six or more pairs of arches, each connecting with a gill; but in modern fishes this number is reduced to four or five as the usual number. Codfish (*Gadus*) has four; dogfish (*Acanthias*), five; primitive elasmobranch (*Hexanthus*), six; primitive elasmobranch (*Heptanchus*), seven. The spiracle of the sharks is their first gill slit, and it is non-functional as a gill. With minor modifications, living fishes continue these relations
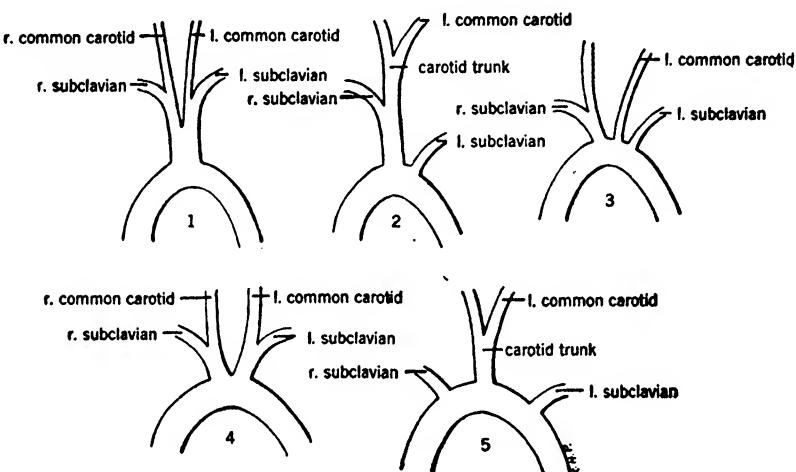
FIG. 163. Some types of branching of mammalian aortae. 1, Perissodactyla, Artiodactyla; 2, Marsupialia, Carnivora, Edentata, Rodentia, some primates; 3, Monotremata, Homo, Sirenia, some bats; 4, some Cetacea, Insectivora; 5, walrus of the Pinnepedia, African elephants.

of the arches, although the lung-fishes break the continuity by leading the blood of the sixth arch back to the heart after its contact with the airsac. The arches are usually numbered by starting with the pulmonary as number six, and continuing anteriorly.

Arches of Amphibia. — The arches of the Amphibia are changed by new tetrapod features (Figs. 165, 166), principally the introduction of lungs as the main aerating structures, and the diminishing importance of the gills. The elongation of the neck and the new position of the heart in its relation to the pharynx stretch the arches and change their proportions. There are two different conditions in the amphibians: first, the aortic system of those that remain in water and retain the gills permanently; and second, the loss of the gills in some adult urodeles and anurans. *Urodeles*, retaining the gills permanently, make some suggestive shifts in the aortic system: (1) the connection of the sixth

aortic arch with the lung is established, but the dorsal connection with the dorsal aorta is retained as the ductus arteriosus (ductus Botalli); (2) arches second and third lose their connection with thé gills, since these gills haⴎe disappeared, and begin the development of the future
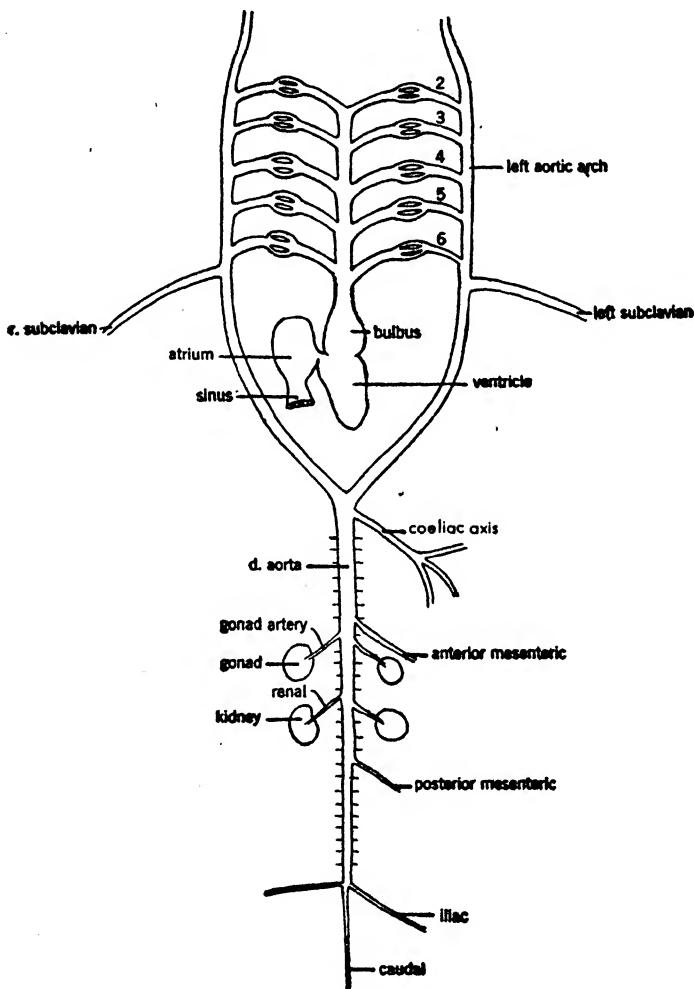
FIG. 164.   Diagram of arterial circulation of a shark.

carotids; (3) the two dorsal aortae are still continuous with no breaks. The anuran (Fig. 166) continues changes started in the urodeles, chang- ing the primitive arch system in the following regions: (1) a further reduction or loss of the ductus arteriosus, connecting the sixth aortic arch (now the pulmonary) with the dorsal aorta; (2) a break in the conti-

nuity of the dorsal aorta, between arches third and fourth; (3) loss of the fifth aortic arch — an established condition in which the sixth arch supplies the lungs, the fourth arch becomes the systemic, and the third and the rest of the arches become parts of the carotid system.
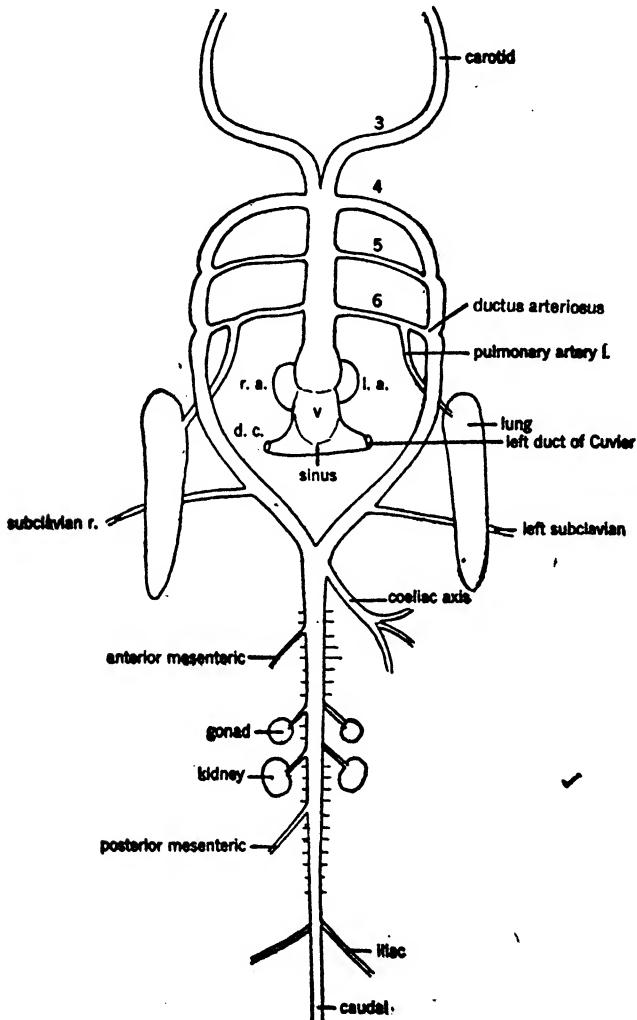
FIG. 165. Diagram of the arterial system of an amphibian (urodele).

Specializations also occur to establish the cutaneous system of the Amphibia. The above changes are closely associated with other changes occurring in the region of the heart and in the vessels that leave it (Figs. 165, 166).

Arches of Reptiles. — With the gills entirely gone, the arches of the Reptilia become fixed in pattern for a lung system, since the gill system is entirely suppressed. The elongated neck region and the separation of the heart from the pharyngeal region have had a decided effect on the proportions of the arches. The following conditions have become fixed:
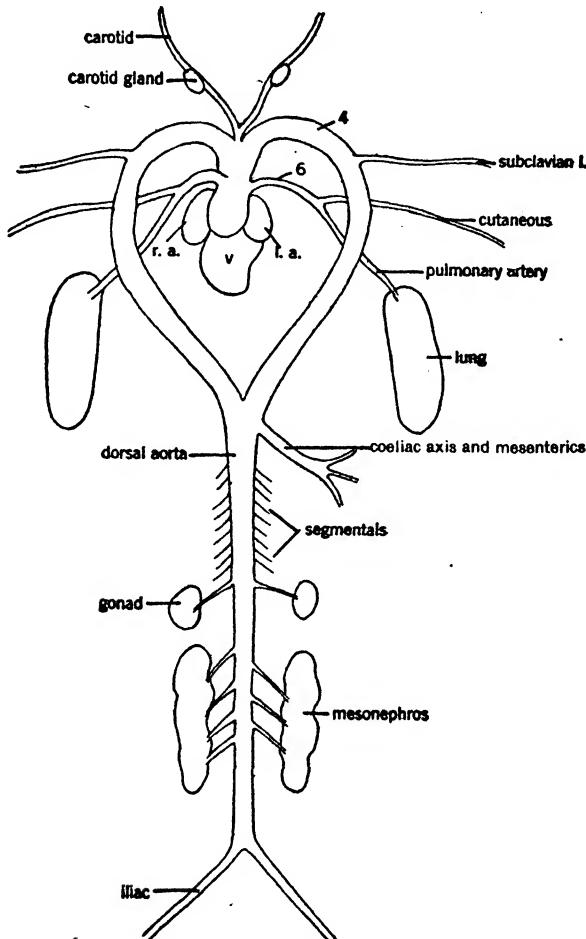
FIG. 166.   Diagram of the arterial circulation of an amphibián (frog).

(1) more complete separation of the ventral aorta into two groups of vessels as they leave the heart; (2) loss of the fifth arch; (3) reduction or loss of the ductus arteriosus, connecting the dorsal parts of the third and fourth arches; (4) elongation of the aortic system (Figs. 161, 167).

Arches of Birds and Mammals. — Both birds and mammals retain but a single systemic arch, the right in birds and the left in mammals.

The vessels leading from the heart are completely divided, so that there
is no intermixture of blood at any place in the system.   As all the
intermediate links are gone, and no remnant of the connection be-
tween the arches is retained, all the blood must leave the right ventricle
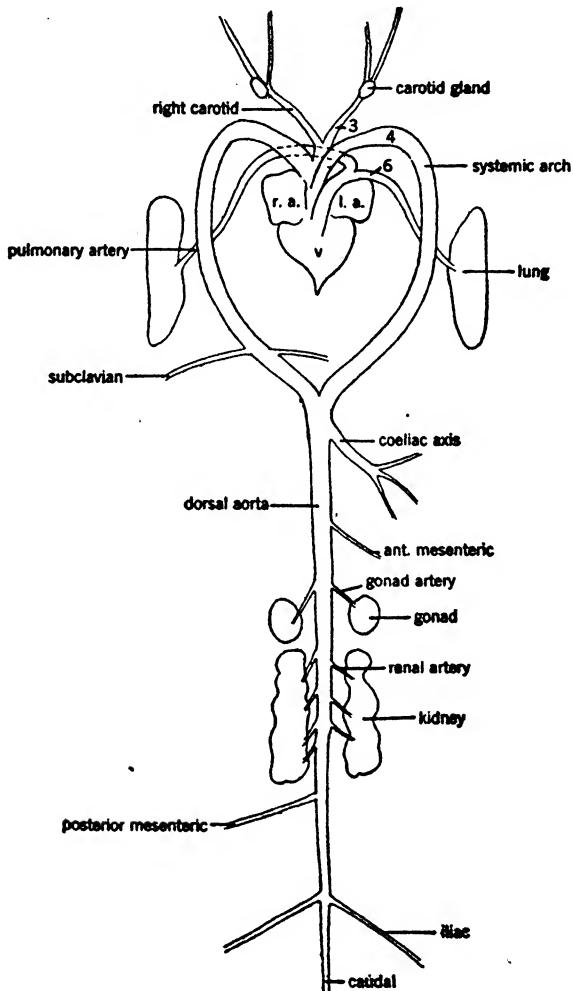
Fig. 167.   Diagram of the arterial system of a reptile (lizard).

through the pulmonary artery and the left ventricle through the single
aorta.   The aortic arches are very important and interesting from
the embryological standpoint, since those of the embryo are of the
primitive fish type but gradually shift to the adult condition (Figs. 160,
168, 169).

Venous System

The venous system is the route by which the blood returns to the heart from different parts of the body. There have been many changes in this system in the development of the vertebrates from fishes to mammals. Originally, it is a paired, rather symmetrical system, but
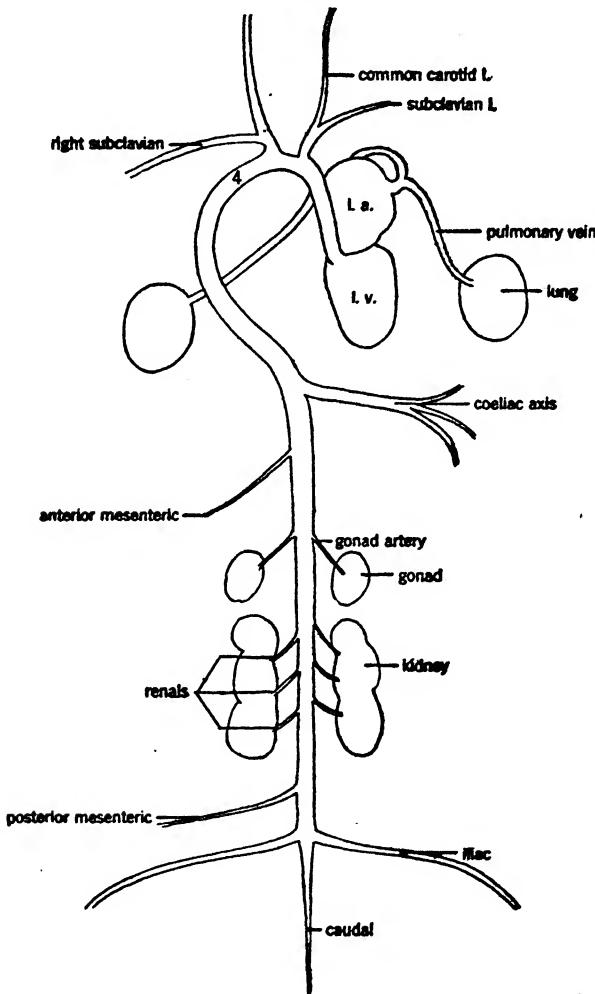
FIG. 168. Diagram of the arterial circulation of a bird.

with the changes due to land life and air breathing, it is forced over to the right side of the body. Its history shows many parts that, rendered useless by elimination of the original structures, have been either changed and used for other purposes or dropped out altogether.

The shark may be taken as a type of the simple symmetrical venous system with most of its parts paired. It consists, first, of two pairs of cardinal veins, the anterior and posterior, which are laid down early in embryonic life. Blood from the head returns to the heart through the anterior pair, and blood from the posterior parts of the body returns through the posterior pair. The blood from the lateral walls and the
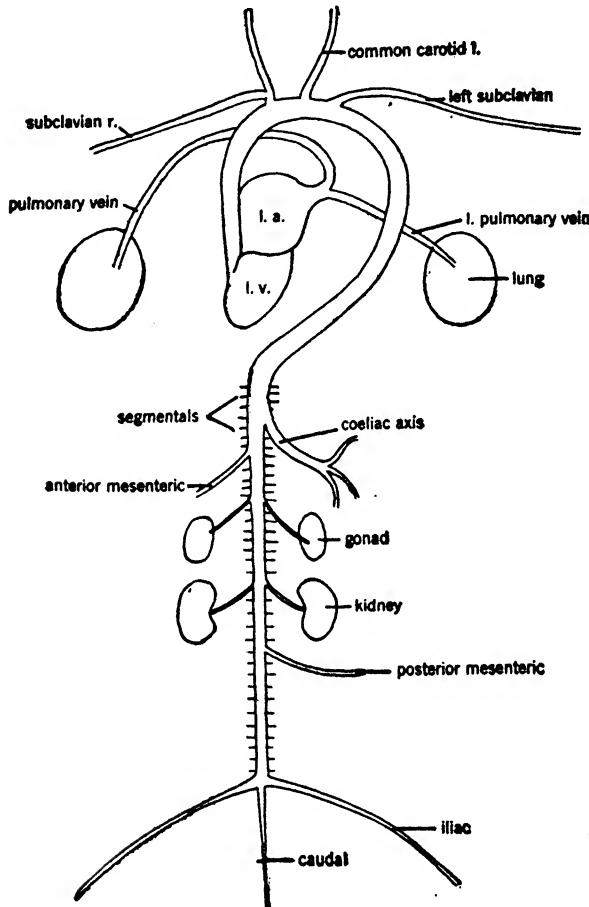
FIG. 169. Diagram of the arterial circulation of a mammal.

pelvic fins returns through the abdominal veins. The caudal region is drained by the caudal vein, a branch of which forms the renal portal and conducts part of the blood to the kidneys. The blood from the alimentary canal returns through the liver, by vessels which break up into capillaries in the tissue of the liver and are collected again in the hepatics which lead to the sinus venosus. The subclavians enter in

the region of the Cuvierian ducts, which form the entrance way into
the sinus venosus.   The shark system is almost diagrammatic in its
simplicity when considered as a whole (Fig. 170).
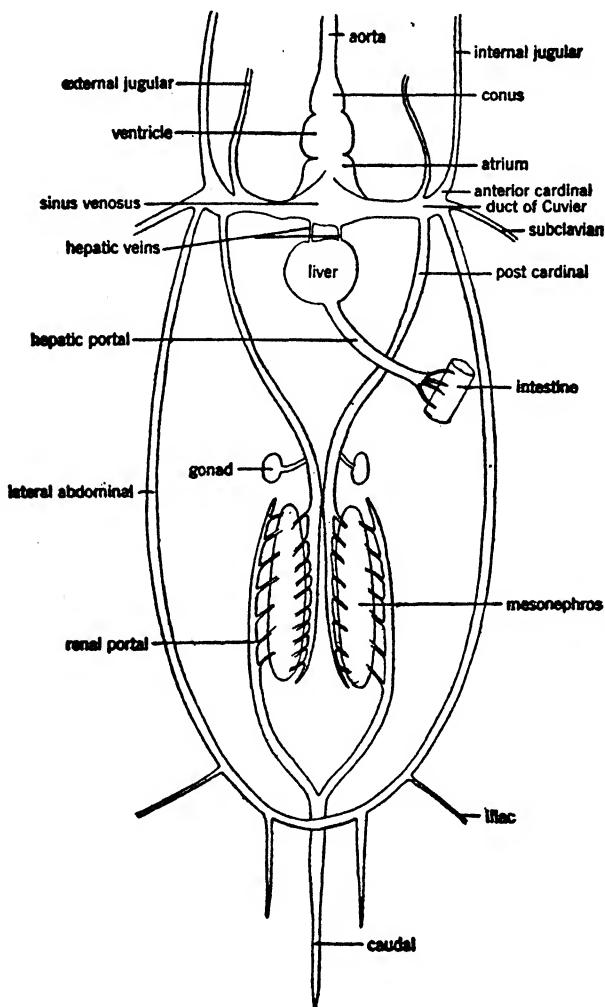
FIG. 170.   Diagram of the venous system of a shark.

The circulation of the urodeles (Figs. 171, 172) resembles that of the
fish, but there are a number of changes due to the shift from water to a
semi-land life.   The anterior cardinals become the jugulars and, losing
their sinuses, empty into the Cuvierian ducts.   The postcardinals, while
functioning much as in the shark, are slowly being reduced in importance

by the growth of the postcava, which is to supersede them (Fig. 171). The postcardinals are beginning to reduce in size, although still retaining their original connection with the mesonephros and the posterior part of the body. The newly established abdominal vein, connected with the vessels from the legs, delivers a part of this blood to the hepatic portal vein. The abdominal vein appears to be formed from the lateral
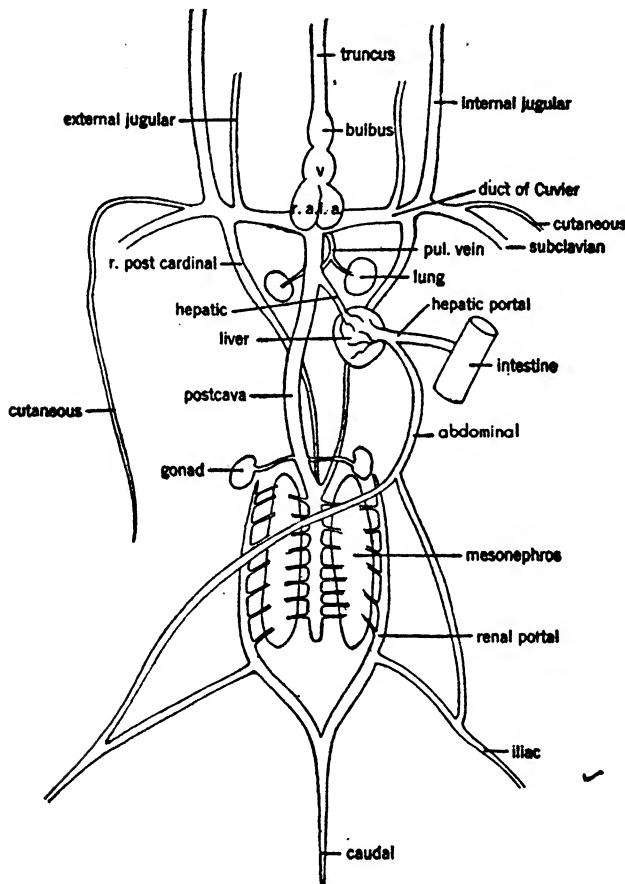
FIG. 171. Diagram of the venous circulation of an amphibian (urodele).

abdominals of the shark, but they have made new connections and established a different subsystem. A new vessel, the postcava, which first appeared in the lung-fishes, has now established itself as the main vessel from the mesonephroi. It drains the blood from the kidney and liver and empties into the sinus venosus direct. Eventually, this vein is to return all the blood from the posterior part of the body. The lungs are

small and not large enough to supply oxygen for the body, and two large cutaneous veins extend along the sides of the animal, somewhat similar to the lateral abdominals of the shark. The lung circulation, also started in the lung-fishes, is well established and a definite system. The cutaneous blood comes from the pulmonary artery and is returned through the duct of Cuvier.| The anuran venous system (Fig. 172) has
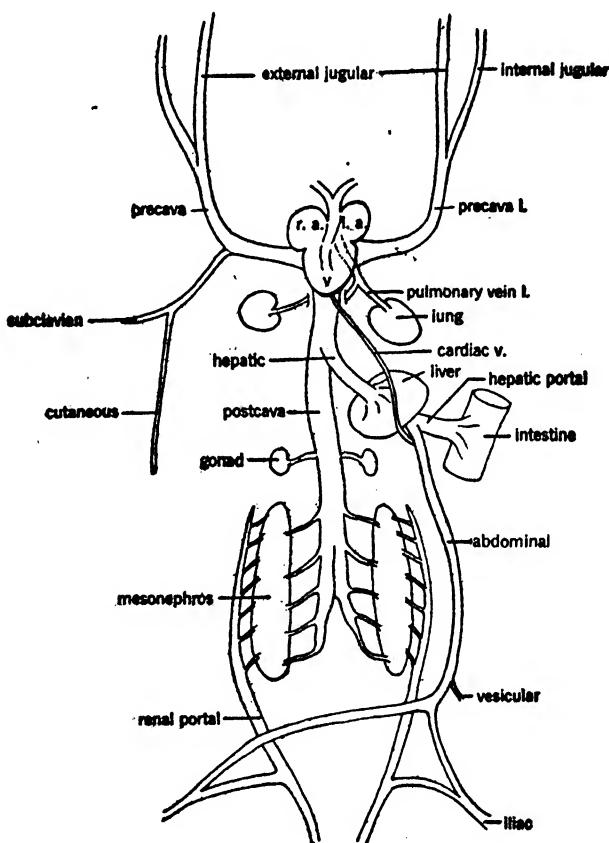
FIG. 172.   Diagram of the venous system of an amphibian (frog).

lost the postcardinals entirely, which forces all the blood through the now thoroughly established postcava. The ducts of Cuvier approach the heart mesially, getting closer to the right atrium. Most of the remnants of the original gill system are lost in the adults. There has been considerable simplification in the anurans, and there is less indication of the older segmental vessels of the more primitive vertebrates. There is a marked increase in the arterial and venous vessels of the limbs.

There is a gradual shifting of the venous system to the right side of the body in reptiles because of the more thorough division of the heart (Fig. 173). Several changes appear to be related to land life, particularly the supply to the limbs. The anterior cardinals have joined to form the jugulars, a condition that is to continue in birds and mammals. The postcava has assumed the entire responsibility for returning blood
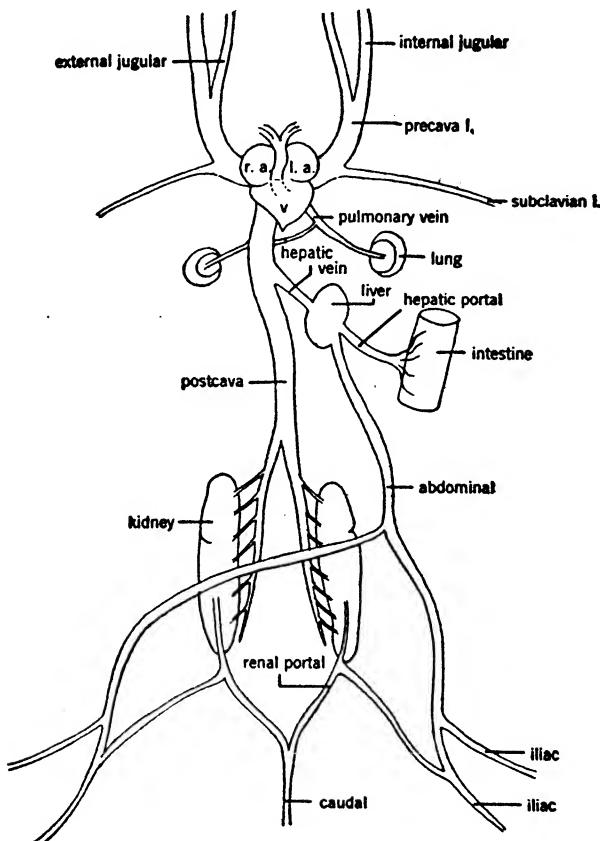
FIG. 173. Diagram of the venous system of a reptile.

from the posterior end of the body. Blood from the posterior limbs is still able to reach the heart through the renal portal system or through the abdominal vein. The renal portal system is retained, but is losing its function, since less of the blood is being taken around the kidney tubules. The hepatic portal system, after going through the liver, leads into the postcava by the hepatic veins. Shifts in the heart have already been mentioned. The cutaneous system of Amphibia has

entirely disappeared as a special part of the respiratory system. The postcardinals are lost in the adult, having disappeared entirely or masked themselves as small vessels drawing blood from the body wall. Naturally, in a group that has so many different forms, there is a wide range of variation in the blood system associated with specializations; thus the snakes have lost one pulmonary vein, and vessels from the non-existent limbs fail to materialize.

The venous system of birds (Fig. 174) is pushed slightly to the right and is somewhat modified from the reptilian type, although it shows the reptilian origin very plainly. The united jugulars form a trunk leading to the heart, and there is often an anastomosis between the right and left sides.— perhaps an advantage when the neck is turned. The ducts of Cuvier are included in the walls of the right atrium and are no longer separate structures. The postcava continues to return the blood from the body and adjacent parts and is the main vessel bringing blood from the posterior end of the body. Because of the added importance of the limbs, especially the wings with their enormous musculature, there is a decided increase in the size of the subclavians and the iliacs of the hind legs. The caudal is tiny, and the renal portal has about the same relations as in reptiles, but probably little or no kidney action is concerned, since the renal portals tunnel through the kidney substance as they did in reptiles, but with little connection with the tubules. Some recent research has questioned this lack of action by the kidneys on the blood carried by the portal system. The abdominal of the reptiles does not appear, but a similar vessel, the coccygeo-mesenteric, drains the blood from the mesenteries and returns it to the hepatic portal. It is possible that it is an entirely new vessel. An epigastric connects the caudal region with the hepatic veins.

The mammalian venous system is rather simple in plan but not in detail. The complete division of the heart into two halves has made a decided change in the return of the blood, and in this it is simpler than in the lower forms. All the blood from the head and anterior limbs comes to the right atrium through a superior vena cava, which may be double or single. The jugulars and the subclavians unite, forming innominate veins, so as to simplify the return of the blood from this region. In many animals the blood from each side of the head and from each fore limb returns separately, through the original two venae cavae. The posterior entrance to the heart through the postcava is retained with some simplification of the venous routes. All trace of the renal portal system has disappeared, and the epigastric is small and completely changed in function. The hepatic portal functions as it does in all vertebrates, delivering its blood to the postcava just posterior

to the heart.   The azygos vein, the remnant of the two postcardinals, functions as a return way for the blood from the body walls (Fig. 175).

A history of the venous system carried through the vertebrate classes
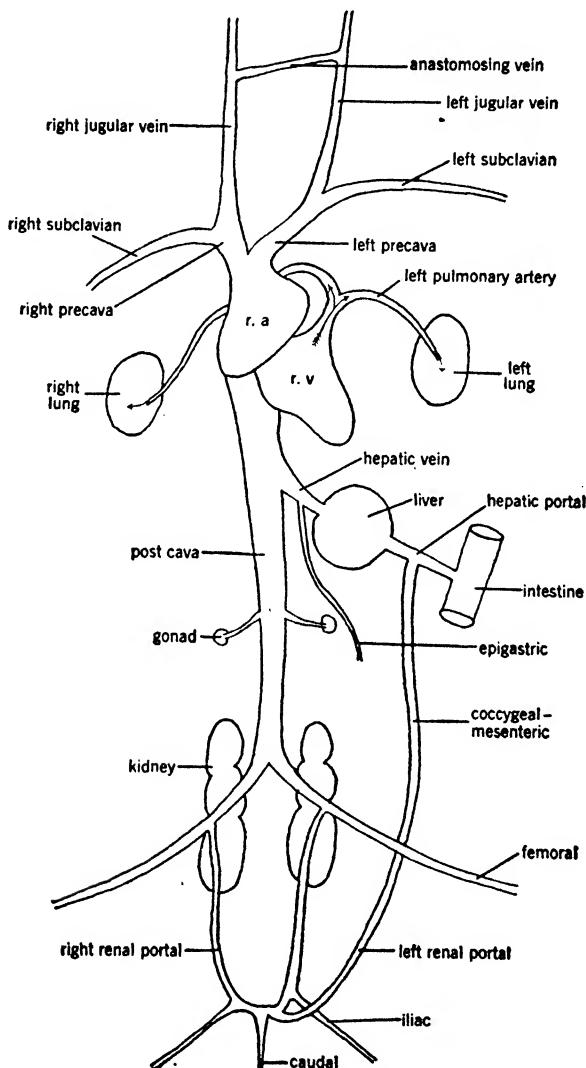
FIG. 174.   Diagram of the venous circulation of a bird.

shows that, from a paired, symmetrical structure in the fishes, there has been a gradual shift to the right side of the body and the development of an asymmetrical system.   The shift is complete in birds and mam-

mals. The system has followed all the changes of the heart, and has simplified its plan as the gills disappeared. As structures drop out and functions change, the vessels either find other territory to draw from or become vestigial and finally disappear. There is much variation within the placentals, and some striking conditions of the veins in marsupials and the monotremes suggest traces of reptilian ancestry. There have
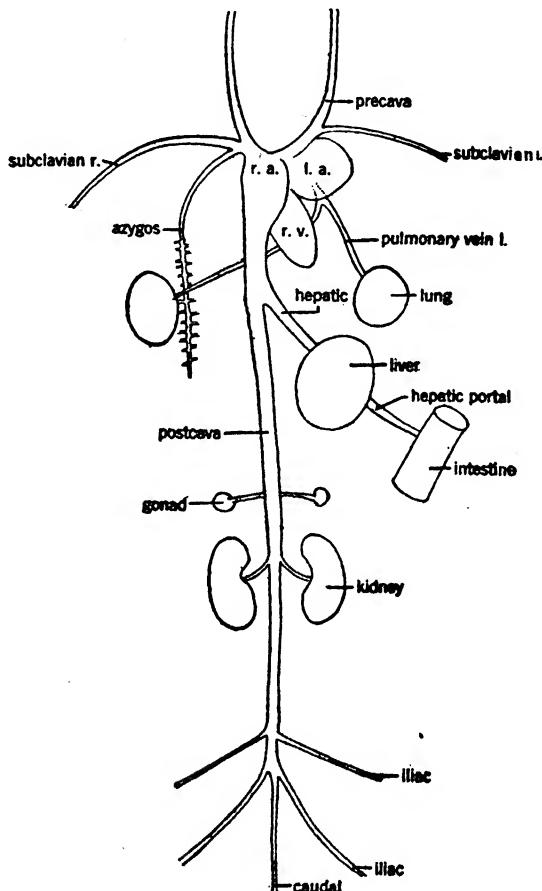
Fig. 175. Diagram of the venous circulation of a mammal.

been so many changes in the system at the different levels of vertebrate history that the story of any individual part becomes enormously involved, by the time that the placentals are reached. Developmental studies, though helpful, often fail to show clearly what has happened in the past. The history of the composite blood vessels will always be an interesting problem for the biologists.

Arterial System

Primitively, the arterial system was strongly segmental, but in vertebrates this has been modified so that little remains to show the original structural pattern. Remnants still appear as small vessels, but they are so insignificant that they are hardly recognized as such. The vertebrates tend to establish large trunk lines to regions where the supply is needed, and thus eliminate the need of small vessels. The arterial system changes much less than the venous, and there is a general similarity in the arterial branches in all classes of vertebrates. The most striking changes occur in the aortic arch system. (See aortic arches.)

The vertebrate body may be divided into three regions of interest, the head and neck region, the aortic arch, and the lung and body region. The head and neck always have special vessels, and this set of vessels becomes more prominent as the neck and head become more distinct from the body. The head always has its own vessels, the carotids for a supply and the jugulars for a return. The carotid system of the shark is rather small, since the supplying aortic arches are so close, and it is difficult to make exact homologies with the similar vessels in tetrapods. An internal vessel supplies the brain and brain case, and a superficial or external carotid supplies the rest of the head. Because of the close proximity of the aortic arches, other vessels creep into the head region, but these are eliminated as the neck becomes more extended. The brain receives a part of its arterial supply from an artery that comes through the foramen magnum. The internal carotid of the elasmobranchs enters the brain case through a foramen just posterior to the optic chiasma and joins with the vessel that comes through the foramen magnum, thus making an anastomosis with the blood system that lies ventral to the brain, the circle of Willis, and the meningeal branches. The external carotid supplies the head region outside of the brain case, including all the superficial regions. It is rather difficult to determine the relations of these vessels to the carotids of the tetrapods, and we may assume that numerous changes took place before the tetrapod series emerged.

The carotids are somewhat puzzling in the lower urodeles (Fig. 165), since they have retained a part of the gill system; but in anurans, the picture becomes more clear cut, with paired common carotids that bifurcate to form internal and external branches. The carotid stem now comes off the fourth aortic arch and is formed from parts of the lost second and third arches. The subclavians originate well anterior on aortic arch four, but they are separated from the carotids. Among tetrapods, there is often a close association between the carotid stem and the subclavians (Fig. 166).

There is a wide range of variation in the reptiles, in which the sub-clavians may be completely separated from the carotid stem. *Lacerta* has a common carotid formed from the third aortic arch, and there are two symmetrical stems from which the internal and external carotids take origin. The subclavians originate far down on the stem of the fourth arch, this having no relations at all with the carotids. *Varanus* has a single carotid stem from which the common carotids originate; *Emys* has the subclavians and carotids of each side coming off together. Some peculiar conditions are found in the limbless reptiles, where the subclavians are entirely absent (Figs. 161, 162).

In birds (Fig. 162), the paired carotids originate from large innomi-nates, each of which gives off a subclavian and common carotid for its side. Since only the fourth aortic is present, the type is somewhat fixed. The carotids really appear to come off from the subclavians. The com-mon carotids extend to the head region before dividing into internal and external branches.

The carotids come from the left fourth aortic arch in all mammals and are usually somewhat related to the subclavians. There is a great deal of variation among the mammals themselves in the relations of these two sets of arteries. The external carotids extend along the side of the head, staying rather close to the lateral side of the skull, and in the alisphenoid region may be encased in a sheet of bone which forms an alar or alisphenoid canal. The internal carotid is given off at the posterior part of the skull and enters the posterior lacerum foramen to supply the brain and its coverings (Fig. 163).

The aorta posterior to the heart extends posteriorly to the tail region, if a tail is present, or forms a vestigial caudal if the tail is missing. There is a great similarity in the vessels given off by the aorta after it starts down the body. Along its length, there are always small vessels that have the character of segmentals, but they are small and insignifi-cant. A shark has a well-organized system of aortic arteries that supply the body cavity, tail, and posterior fins. The number of branching arteries is really surprisingly small for a fish at the lower end of the fish group. Small segmental arteries that supply the back muscles and the spinal cord enter the body wall along the greater part of the length of the aorta. Inside the body cavity, the coeliac axis is first, supplying the anterior part of the digestive tube and the liver. An anterior mesenteric supplies the posterior part of the digestive tube and spiral valve; a third, the lienogastric, supplies the spleen and a part of the digestive system. The mesonephros is supplied by small segmentals along its length. An iliac supplies the posterior fin. In both fishes and amphibians, this grouping of the arteries is similar. The gonads have their own,

and in mammals, the renal arteries are reduced to one for each kidney. Elongated animals show the coeliac merely as one of a series supplying the length of the digestive tube. *Siren, Cryptobranchus*, and *Necturus* show varying degrees of this type of distribution to the alimentary canal. A frog, however, has a well-defined coeliac axis. Numerous changes in the arteries occur in connection with the development of limbs, and the arteries keep pace with the limb development. In mammals, there is much similarity in these trunks, since they supply structures of a like type and position. The trunk arteries come off both as single or paired branches, since paired organs usually have paired vessels. The coeliac axis, anterior and posterior mesenteries, are single trunks; while those that supply the kidneys, ovaries, testes, lumbar and leg regions are paired. The abdominal aorta of the dog has the following branches: series of intercostals; coeliac axis; anterior mesenteric; phrenico-abdominal; renal and spermatic; iliac; internal iliac. Those going to paired organs have paired trunks. In man a similar line of arteries supplies the body, and, with minor variations, the same system is to be found generally in the mammal group.

Lymph System

The lymph system was first observed about 1627 by an Italian named Aselli, who saw the prominent vessels in the mesenteries of a dog and assumed that they were lacteal veins, carrying material to the liver. Later in the century, this mistake was corrected and their true nature was established. The system has always been troublesome, and even today, there is little agreement on the origin. One school has shown from its researches that the lymph system is an outgrowth from the venous system; another group has shown that the system is an ingrowth that develops and finally makes its connection with the venous system. Regardless of its developmental history, it is safe to assume that, at all times, in vertebrates, the lymph system has been an integral part of the circulatory system. The history shows that there have been numerous changes in detail but that the system continues to perform the same function, that of leading the blood fluids to the cells and tissues and returning these fluids back to their blood stream.

It is difficult to demonstrate very much of the lymph system in elementary courses, though the vessels of the mesenteries are easily seen. The thoracic duct is easily observed in the cat and rabbit, and has a diameter of three or more millimeters in the dog. Blood capillaries extend into all tissues and organs, but they do not come in direct contact with the spaces surrounding the cells themselves. The small, tissue-filled spaces

that surround the cells themselves have a supplementary blood system that brings them in direct contact with the supply, so that they can have the varied materials that they need for their activities and return the wastes to the venous system for elimination. The cells of the different tissues have varied requirements, and each picks what it needs. Throughout the vertebrates, a lymph system performs these necessary functions. The capillaries of the blood system take the blood to the region of the cells, and at all times a part of the blood fluid is escaping from these vessels and also being taken back into them. The main entry way of the whole lymph stream in mammals is through a pair of ducts that enter the venous system through, or close to, the subclavians, where the pressure is low. In man the left thoracic duct is usually the
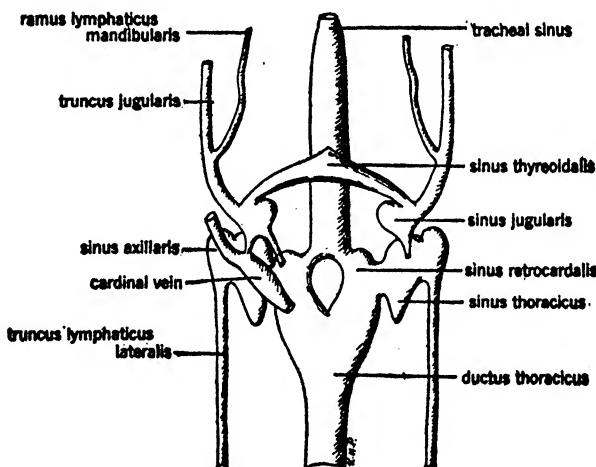
FIG. 176.   Schema of the lymph sinuses of a lizard (Lacerta vivipara). After Hoyer.

main functional entrance. Lower animals have other connections and, besides the thoracic ducts, connect at the iliac veins and in other places in the body cavity. Stomata have been described among the viscera and mesenteries of man and other animals.

The amount of material going through the lymph system is much smaller than that of the blood circulation, and its movement is much slower. Although it has a regular circuit, its progress must depend upon incoming lymph pushing from the rear and from pressure influenced by the muscles and tissue in which the lymph vessels are imbedded. However, the lymph vessels themselves have some resiliency, and some parts are supplied with smooth muscle and connective tissue. In lower animals, the lymph hearts, which are valved, have more regular move-

ments. It is estimated for the dog that 1.3 per cent of its weight goes
through the system in 24 hours.

The lymph fluid is colorless and resembles dilute blood since the blood
is its original source. Its food materials are those carried by normal
blood, and it gathers up wastes from the cells to be returned to the blood
stream for elimination. It has some slight clotting powers, but it is
much slower in this respect than blood. Leucocytes enter the stream
freely, but under normal conditions the erythrocytes (red corpuscles) do
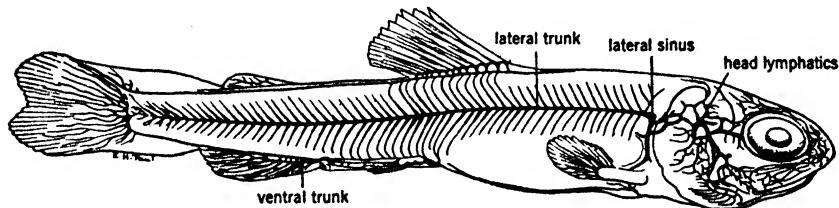
FIG. 177. Lymph system of an embryo trout. After Hoyer and Michalski.

not. If the pressure of the venous system is raised, there is a corre-
sponding back pressure on the lymphatic system, with a swelling of the
tissues and other visible manifestations of its presence.

The lymph vessels are much lighter than veins but have some smooth
muscle and connective tissue; valves are scattered through the system;
and stomata, connected with the coelom, have been described.

Lymph nodes, characteristic of the system, intercept the lymph
vessels along their length. These nodes vary from the size of a pinhead
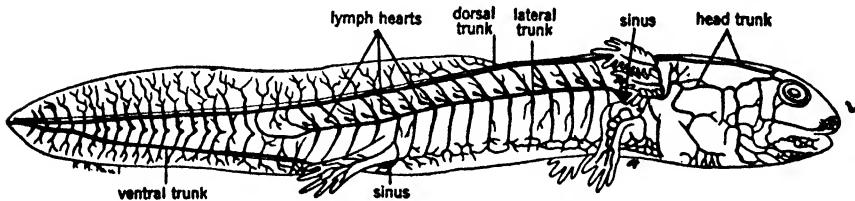
FIG. 178. Lymphatics of a salamander larva. After Hoyer and Udziela.

to that of a bean, and even the superficial nodes are not noticeable
externally. Those under the jaw may be felt as oblong flattened bodies.
If for any reason they become inflamed, the superficial nodes become
very conspicuous. These nodes are supplied with a vascular system
consisting of a vein and an artery, and afferent lymph vessels which
break up into sinusoids in the nodes before entering the efferent vessels.
In these nodes, the lymph is filtered, and cleared of bacteria and other
substances that may have got into the lymph stream.

Lymphocytes are formed in these nodes. When bacteria become too plentiful the nodes break down, become inflamed, and are an evident danger signal. The nodes are numerous in the axilla, groin, neck region, and throughout the body cavity, so that practically every system and organ is well supplied except the deep parts of the central nervous system, the bone marrow, and possibly other structures. Haemolymph glands are associated with the carotids and some of the large veins, but they are not glandular in structure. They differ from lymph glands in containing red corpuscles.
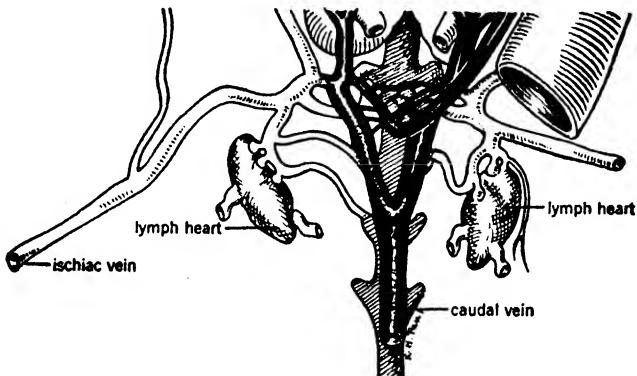
FIG. 179. Lymph hearts of an alligator. After Spanner.

Both the palatine and pharyngeal tonsils are of the typical lymphoid tissue and function as lymph structures. The tonsils of the palate are oval bodies imbedded in the walls of the upper pharynx. They have numerous pits and depressions and a series of complicated crypts around which the lymphatic vessels are grouped. The pharyngeal tonsil is posterior to the Eustachian tube and along the roof of the pharyngeal cavity.

The largest and most prominent lymph structure is the spleen, which lies close to the stomach in the body cavity, although of course it has nothing to do with digestion. It is of variable color, ranging from brown to a deep purple, and is always in contrast to the colors of the digestive tube. It is highly vascular, being well supplied with arteries and veins, and is made up of spleen pulp, which covers a trabecular network, so that it is able to fill and empty rapidly. It may serve as a blood reservoir and a producer of lymphocytes. Under certain conditions it is removed, and then the body appears to have lost one of its protections against infections and is less prepared to meet physiological changes. In some fevers (malaria) the spleen becomes enormously enlarged, so that it pushes out on the body wall. Patches of lymph

follicles of varying size appear in the small intestines of the higher vertebrates and may occur in the large intestines. They are isolated follicles in the lower animals, but in reptiles, birds, and mammals they form larger aggregates, known as Peyer's patches. In a horse, these may be an inch or more wide and fifteen inches long. (See Chapter VI.)

Lymphatics of the fishes that have been studied show an extensive superficial series of lymph vessels, along the sides of the body and extending into the tail and fins (Fig. 177). In the body cavity, the lymph vessels parallel somewhat those of the venous system. Instead of the one main entrance into the venous system, as in mammals, there are several openings, at the anterior, middle, and posterior ends of the body. Usually, lymph hearts are not present in fishes, but a few have been described. |Urodeles resemble fishes in the plan of the lymph system (Fig. 178), and generally have a pair of pulsating lymph hearts that open into the iliac veins, while numerous small sinuses take the place of hearts in the system| Anura have two pairs of pulsating hearts with valves, the posterior pair opening into the iliacs, and the anterior pair into the vertebral branch of the jugular. Reptiles retain but the posterior pair of lymph hearts, which connect with the iliacs (Fig. 179). In mammals and birds, the hearts are lost and the main opening into the venous system is through the thoracic ducts, which usually open into the subclavian veins, a region of low blood pressure. In man there is but one functional duct, the left.

Résumé ·

The blood of vertebrates circulates in a closed system. It transports food materials, removes waste materials, regulates the temperature of the body, carries hormones and enzymes, forms substances that combat diseases or produce immunity, supplies oxygen to the tissues, and removes carbon dioxide. The heart is a muscular organ, with spring-like coiled muscles that contract in systole and relax in diastole. The blood supply of the heart itself comes through coronary vessels. The innervation is through the autonomic system and the vagus nerve. Fishes have a two-chambered heart which receives only venous blood (except in lung-fishes). Amphibians have a three-chambered heart, the atria being separated, as some blood returns from the lungs to the heart. Reptiles have a three-chambered heart with a partial division of the ventricle. In birds and mammals the separation of the ventricles is complete, so that the heart is four-chambered. In a four-chambered heart both atria contract at the same time, and then both ventricles contract, and the beat is regulated by the atrio-ventricular bundle, or timing apparatus (the bundle of His). The aortic arches, primitively six, are reduced and changed when the gills are replaced by lungs — the sixth pair becoming the pulmonary arteries; the fifth pair being lost; the fourth pair forming the systemic vessels, or aortae; and the

third pair, with parts of the second and first, becoming the carotids. The right side of the fourth aortic arch is retained in birds and the left in mammals. The arterial system always remains relatively simple in design, with few changes except those of the aortic arches; the venous system, however, at first symmetrical, is gradually shifted to the right as the evolutionary scale is ascended. The main vessels of the venous system in fishes are the anterior and posterior cardinals. In higher vertebrates a postcava replaces the posterior cardinals, and the anterior cardinals become the jugulars. Fishes have two portal systems, the hepatic and the renal. The lymph system, which collects the plasma that has escaped through the capillaries into the tissues and returns it to the venous system through the thoracic ducts, consists of a network of lymph vessels, lymph nodes, Peyer's patches (in the walls of the intestine), and other lymph tissues, such as the tonsils and spleen. The lymph itself clots slowly; it bathes tissues, supplying them with food and removing waste, carries fats from the intestines to the venous system, neutralizes toxins (especially in the lymph nodes), and forms a very important part of the vascular system.

CHAPTER VIII

RESPIRATORY SYSTEM

Because of thick body walls and impervious coverings, such as scales, dermal plates, feathers, or other integumental materials, all vertebrates require some special means of respiration for supplying oxygen and removing carbon dioxide. In land animals this process is carried on through moist membranes of the lungs or other parts of the body. The gills of fishes are composed of lamellae in which the blood is exposed to the water through a thin membrane that permits an interchange of gases. Some fishes, such as the climbing perch (*Anabas scandens* and *Saccobranchus*), have accessory gill chambers with additional respiratory surfaces, so that they can remain out of water for some time.

One of the most striking features of fishes is the peculiar airsac or airbladder (Fig. 180), present in all fishes (Osteichthyes) except the elasmobranchs and a few bottom feeders such as the flounders (pleuronectids), where it is lost in the adult stage, although present in the young. There is no certain trace of an airsac in the elasmobranchs, although some investigators have thought that they observed it in the developmental stages. The airsac originates as a diverticulum on the ventral side of the digestive tube in *Polypterus* (Fig. 180 D), laterally in the Dipnoi, and dorsally or dorso-laterally in the teleosts (Fig. 180 A), and may be single, double, ventral, lateral, or dorsal. Several theories have been proposed to explain these variations.
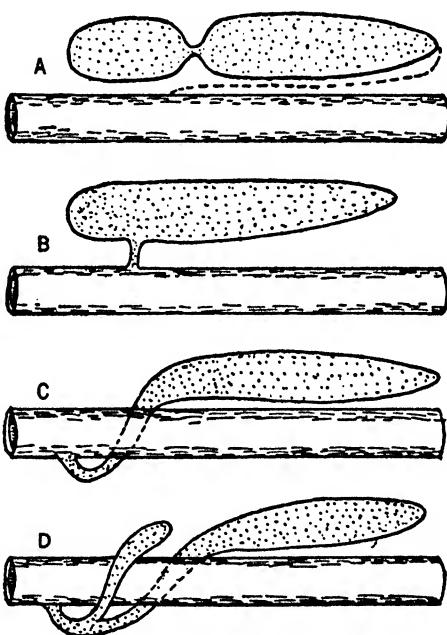
Fig. 180. Diagrams of airsacs in fishes. A, teleost with a closed duct; B, Lepisosteus, open duct; C, Neoceratodus, open duct; D, Polypterus, open duct. After Kerr and Goodrich.

Goodrich suggests that perhaps the most promising is that of Spengle, who thought that the airsacs might be derived from a posterior pair of gill pouches. Migration of these would account for most of the conditions found in fishes.

Intermediate Fishes. The most lung-like airsacs are found in the intermediate fishes, where the structure is usually long, much more than a simple sac, and connected to the throat region by a large-mouthed duct. *Amia, Lepisosteus, Acipenser, Polyodon, Polypterus,* and the Dipnoi (Fig. 180) all have large, prominent airsacs that structurally very much resemble lungs, since they have a large blood supply and also red bodies and gas glands. These gas glands consist of an epithelial layer and an underlying rete mirabile of blood vessels, forming a blood net close to the surface, so that there can be an exchange of oxygen. *Polypterus* has a double sac; *Amia* and *Lepisosteus* have single ones. From our knowledge of their habits, it seems certain that these sacs are very important in respiration. *Lepisosteus,* when caught in nets, is generally found dead because it cannot survive being held under the water for a long period. The Australian lung-fish, *Neoceratodus,* lives in waters that become stagnant; the African lung-fish, *Protopterus,* lives in waters that dry up periodically. At the beginning of the dry season, *Protopterus* burrows down in the mud, forms a slimy cocoon, and remains there until the next flood water, connected with the surface by a small tunnel through which it breathes. These cocoons, with their living contents, are now shipped all over the world.

Teleost Airsac. The teleost airsac is of two types: those in which the pneumatic duct is open (physostomi) (Fig. 180 *B*); and those in which the duct is permanently closed (physoclysti) (Fig. 180 *A*). Those with the open duct can change the air with a gulp, but those with the closed duct regulate the density of the enclosed gas slowly. The airsacs are supplied with gas glands, consisting of a folded, glandular epithelium and its underlying system of blood vessels. The sac itself may be single, constricted to form a double or a triple apartment structure. The herring, a low teleost, has a second duct that opens out near the anus.

The blood supply of the airsacs comes from the sixth arterial arch in *Amia, Polypterus,* and the Dipnoi, while the teleosts supply it from the dorsal aorta. Blood is returned directly to the heart only in the Dipnoi. The innervation is through the vagus nerve and the autonomic system.

Weberian Ossicles. A very interesting and useful specialization of fishes is the development of a series of ossicles, connecting the airsacs with the brain and ear (Fig. 181). These ossicles are peculiar to the Ostariophysi, a group of fishes including the catfishes, carp-like fishes, characins — a South American and African fish — and the electric

eels. When discovered by Weber, they were considered as true ear ossicles and given the same names, but their origin is different, and it is now known that they are modified parts of vertebrae. These ossicles — tripus, intercalarium, scaphium, and claustrum (Fig. 181 B) — form a
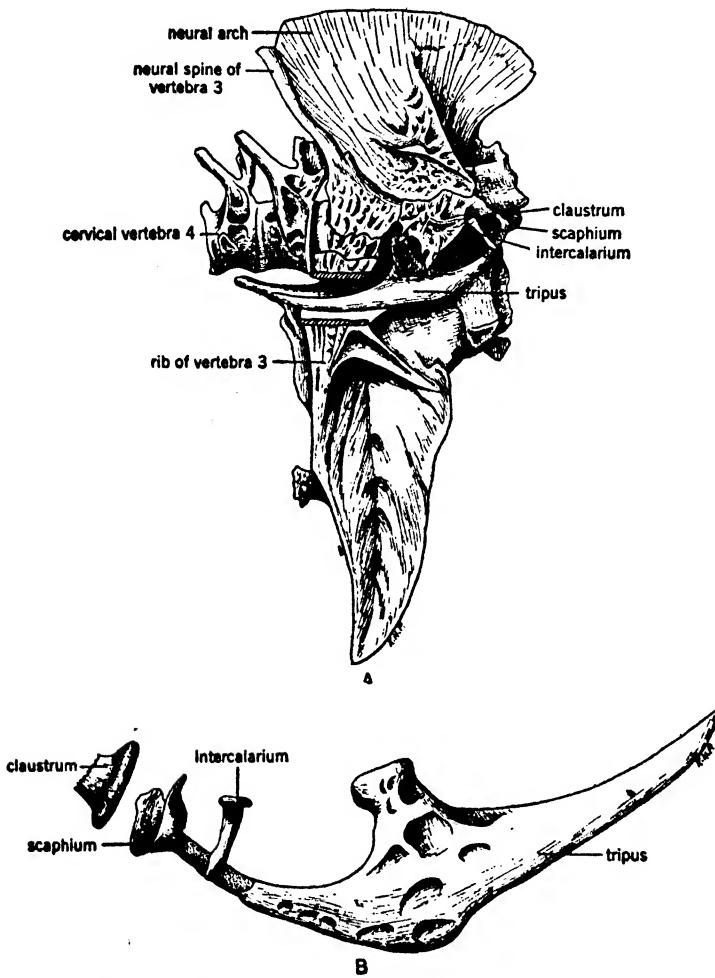
FIG. 181. Weberian ossicles of teleost, Ictiobus urus. A, first three vertebrae dissected to show the ossicles in position; B, the Weberian ossicles.

fine mechanical connection through which the tension or relaxation of the airsac is transmitted to the ear and brain. It has been suggested that they might serve as a manometer, but this may be questioned.

Although originally a breathing organ, the airsac has developed other uses that make it an important fish structure. In the intermediate

fishes, it seems to be entirely an accessory organ of respiration; but in the teleosts, where it serves as a reservoir of oxygen, there are several other uses. The teleost airsac has gas glands which separate the oxygen from the blood. The anterior region of the sac is specialized for gas secreting and the posterior part for gas absorbing, so that the oxygen can be taken back into the blood when the necessity arises. Its use as a pressure gauge is shown by experiments in which a fish is sealed in a glass bottle, with a connecting apparatus to raise or lower the atmospheric pressure. A fish adjusted to a definite pressure can remain at one level with no effort at all, but it becomes out of balance when the pressure is raised and is seen to use the fins to keep at a desired level. ˌThis effort continues until the gas pressure of the sac can be changed and adjusted to this particular pressure. This adjustment is fairly rapid, even in fishes with a closed pneumatic duct. The connection of the airsacs with the brain and the ear adds another function that has been interpreted in various ways. It is thought that this connection may be a special development of the pressure gauge or manometer idea, or an auxiliary to hearing and the action of the ear.

Respiration in the vertebrates is carried on in several ways. Gills are the water type and lungs the land type of structure for this purpose, but other parts also may be used. The ends of the alimentary canal may be vascular, as in the lungless salamanders, and serve for this purpose; in many animals, especially amphibians, the skin is supplied with fine blood vessels and becomes very important in respiration, in fact as necessary as the lungs themselves. Gills are prominent features of fishes and amphibians, but they are lost in reptiles, birds, and mammals. Gill slits are present in the protochordates,. although it is possible that their main function here is divided, since they are also important in food-getting, in connection with a ciliated groove, the endostyle. In *Amphioxus* they probably serve in both ways.

Gill Slits

In the developing embryo the endodermal pouches in the side walls of the pharynx extend to the ectodermal covering of the body wall, to which they grow fast, and become pierced by openings called gill slits. The number of gill slits is variable, with a greater number in the lower forms and a less number in the better-organized forms. *Amphioxus* has about one hundred and forty pairs, the hagfishes from seven to fourteen pairs, the lampreys six, and two primitive sharks, *Hexanthus* and *Heptanchus*, six and seven, respectively. The normal number is five in modern fishes except the teleosts, which usually have four. In

amphibians the number is reduced to three. The anterior gill slit may be modified to form a spiracle, as in sharks and some of the lower fishes, or it may be permanently closed. The spiracle shows its origin by having a small demibranch.

The gill slits open to the outside in several ways. Cyclostomes have sac-like gill pouches, with either separate or combined ducts to the exterior. Sharks have five slits, one for each gill, with a complete septum, while the rest of the fishes have a short gill septum and a flap or bony operculum which covers the whole gill chamber.
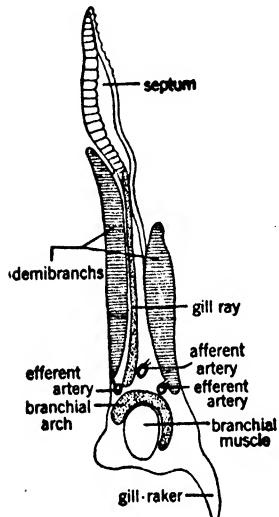
FIG. 182. Section of shark gill.
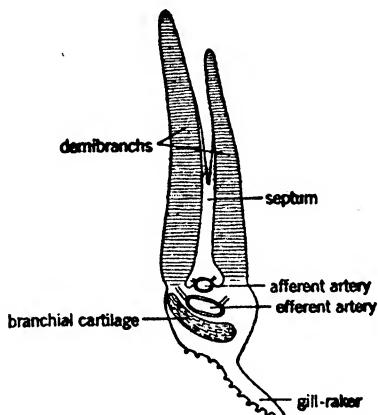
FIG. 183. Section of teleost gill.

Gill Structure

The typical gill, or holobranch, consists of a median septum, with a demibranch in each side, and a supporting structure of either cartilage or bone, which forms the branchial arch (Figs. 182, 183). Branchial rays may extend out into the gill to give it more strength and stability. The gill skeleton also furnishes a basis for the attachment of muscles, and the gills move almost constantly as the water flows over them. The lamellae on both sides have folded surfaces in which the branchial vessels with their capillaries bring the blood close to the water for the exchange of gases. The typical teleost series consists of four pairs of holobranchs, although this number may be reduced (Fig. 183).

The internal openings of the gill chambers into the pharyngeal wall are usually protected by gill-rakers, projections from the base of the gill arches, which prevent food and débris from entering the gill cavities.

These rakers may be small tooth-like projections, or they may be lengthened into long rays as in the paddlefishes (Fig. 184). Many teleosts have developed valves on the sides of the mouth which permit the flow of water inward but prevent an outflow when the mouth cavity is compressed. Water taken in through the mouth is thus forced through the internal gill openings and over the gills. Ventrally the gill region is supported by the combined bases of the hyoid and bran-
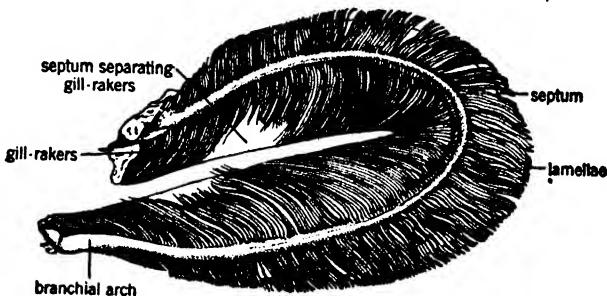
FIG. 184. Gill of paddlefish (Polyodon spathula).

chial arches, and open spaces in the floor may be filled in by a series of branchiostegal rays.

Besides the typical gill structures, two other types appear in vertebrates — external gills and gill filaments (Fig. 185 A, B). True external gills are found in the embryos of lung-fishes and amphibians. The gills of the amphibians are of the external type, present in the developmental stages of all, but lost in those that have become adapted to land life.
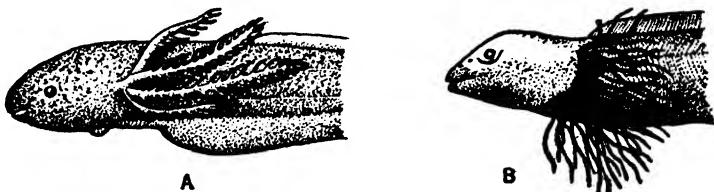
FIG. 185. A, larval ectodermal gills of Lepidosiren paradoxa; B, gill filaments of shark (Gymnarchus niloticus). After Kerr.

The water-living urodeles retain their gills for respiration, since the lungs are usually small, inefficient, and sometimes lost as in the lungless salamanders. In *Necturus* the three pairs of external gills form conspicuous tufts on the side of the neck, which wave rhythmically and are very striking in a living specimen. Thin filamentous gills appear in the embryos of all sharks and in some teleosts. These thread-like gills serve in respiration but may also function in the absorption of food. The

filaments extend out from the lamellae of the gills and have branchial blood vessels corresponding to those in the gills themselves. (See Fig. 185 *A, B*.)

Trachea

The trachea, slightly more than a simple duct in amphibians, becomes a tube reinforced with cartilage in the tetrapods, so as to prevent collapse. The trachea connects the lungs to the pharyngeal cavity, splitting at the lower end into bronchii, bronchioles, and finer subdivisions which enter the tissue of the lung. The pharyngeal opening, the glottis, is a mere slit but comes to be associated with a specialized structure, the larynx, in the higher tetrapods. In amphibians there are two small cartilages on the sides of the glottis and a few unorganized pieces scattered along the length of the trachea (Fig. 288). The reptilian trachea (Fig. 300) becomes completely ringed with cartilage along its entire length, the circles of cartilage being complete in the lizards and some snakes, but in others the dorsal side is of softer cartilage or with an incomplete circle so that it may fit snugly against the esophagus and permit the passage of food along the digestive tube.

Birds, with their elongated necks, have a long trachea (Fig. 310), strengthened along its entire length by cartilaginous rings, that may become ossified. The trachea of cranes and swans is folded and coiled in the keel of the sternum, getting into the sternum during embryonic development. The syrinx, a structure on the lower end of the trachea, between the lungs, is the sound-producing organ of birds. The bird larynx is but little developed. In mammals the trachea is variable, long in the giraffe and very short in the whales and sirenians, where it bifurcates just posterior to the cricoid cartilage of the larnyx. Its lower end divides into bronchii, which subdivide into bronchioles and then smaller ducts which enter the structural units of the lung. The larger subdivisions have cartilaginous supports, but the bronchioles and smaller tubes do not (Fig. 321).

Larynx

The pharyngeal opening, the glottis, which is simple in the amphibians, becomes much more specialized as the higher groups are reached. Reptiles have a well-developed hyoid arch which helps to hold the larynx in position. The reptilian larynx is formed by two arytenoid cartilages and a cricoid. The bird larynx is simple because of the development of a second organ for sound production (Figs. 186, 310). The larynx reaches its greatest development in mammals, where it is a highly specialized sound-producing organ, with a highly developed
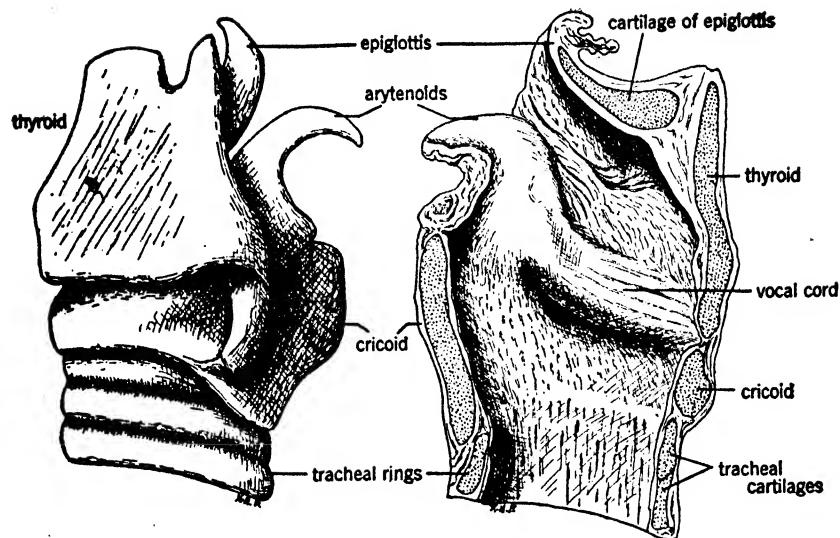
FIG. 186. Larynx of cow. A, lateral; B, sagittal section.
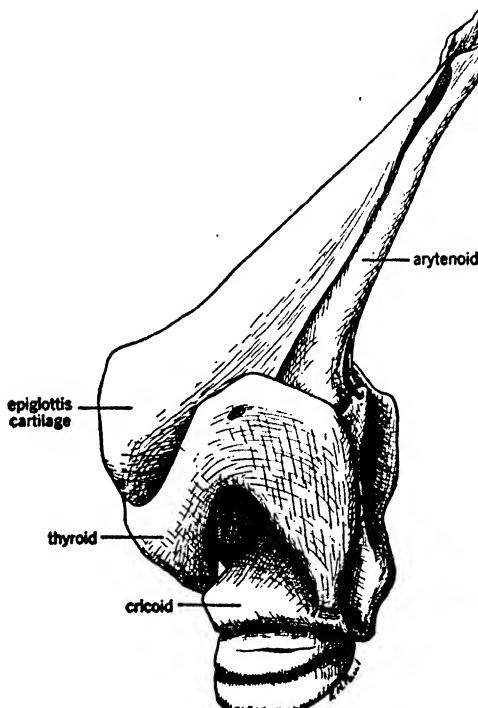
FIG. 187. Larynx of a cetacean (Ziphius?).

musculature. The epiglottis, a mammalian structure, consists of a supporting cartilage, covered with mucous membrane, to form a flap that extends back over the glottis during swallowing but is erect during breathing. Two arytenoids and two cricoid cartilages form the walls, and the thyroid cartilage forms the ventral side. The thyroid cartilage is double in the developmental stage but single in the adult. Besides these cartilages, two other pairs may be present, the cornulate cartilages at the tips of the arytenoids, and a small pair of cuneiform cartilages anterior to the cornulates (Figs. 186, 187, 189).
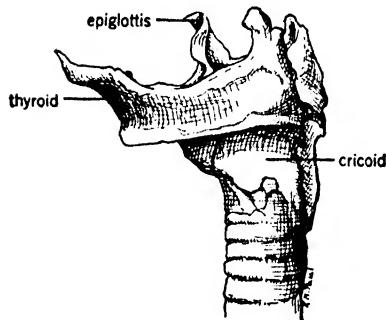
FIG. 188. Larynx of opossum (Didelphis virg.).
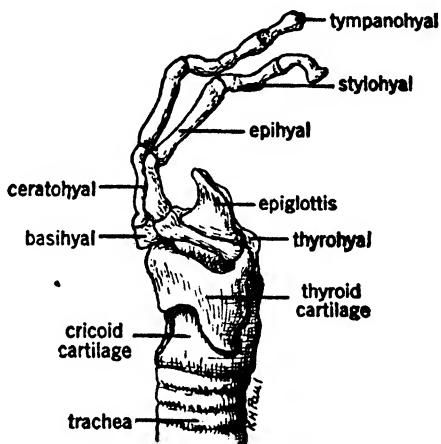
FIG. 189. Larynx of a dog, from the left side. Orig.

Lung

The lung is a constant structure in all land tetrapods and all water forms with the single exception of a family of the Amphibia, the Plethodontidae, in which it has been lost. Most of these amphibians live in mountain torrents, where a heavy, compact body is necessary to prevent being washed away. These lungless forms carry on respiration through the capillaries of the skin, mouth, pharynx, esophagus, and anus. It was indeed fortunate for the first tetrapods that they could make their approach to land with respiratory structures already supplied by their fish ancestors. In spite of the fact that both fishes and tetrapods have gills and airsacs, there is some question as to the homology of these structures. One hypothesis would derive the airsacs of the fishes from a small pouch that originates from the anterior part of the foregut; another would derive them from the posterior pair of gill pouches. The lungs of tetrapods do originate from a small pouch that develops on the

ventral side of the foregut, first as a single sac, then becoming bifurcated to form the double lobes. A happy solution might derive both structures from the posterior gill pouches. Regardless of their homology, airsacs and lungs have a number of common points, such as: both are used for respiration; both are used in water animals to control the density of the body; both may be single or double; both are innervated by the vagus nerve; both are supplied by the sixth arterial arch (tetrapods and *Polypterus* and dipnoans of the fishes). (Fig. 180.) In other fishes, the airsacs may arise from the dorsal or the dorsal-lateral side. It has been suggested that possibly, in the original condition, the blood supply of each was similar, and that both were supplied by the sixth arterial arch and also from the aortic arch, but the shifting of the airsac posteriorly caused the breaking away from the sixth arch, so that in most fishes only the aortic branch serves as a source of supply.

Knowledge of the use of the lungs is comparatively modern, since nothing could be known of the function until the chemistry and physiology were perfectly understood. A real understanding of the lungs starts with the discovery of oxygen and its relation to combustion and oxidation. Before the lungs could function perfectly in tetrapods, a number of shifts and adjustments of a mechanical nature had to be made, and these followed slowly with the development and maturity of the tetrapods. The gulping process of the fishes was a rather uncertain means of filling the airsacs, and although the general plan was the same in the Amphibia, it was modified by a new connection between the nasal sacs and the mouth, a condition started in the Dipnoi. This was completed in the early amphibians, and, with a closing valve on the nostrils, it was possible to use the throat and pharynx to force air into the lungs, and to utilize the elasticity of the lung structure to help in expelling the air (Fig. 288). There is a steady improvement in this process of supplying air to the lungs that follows through the reptiles (Figs. 190, 191) and reaches its perfection in the birds and mammals. A few reptiles have a secondary palate that pushed the posterior nares closer to the pharynx (Crocodilia). The gas glands of fishes gave way in the tetrapods, to a finer structure, a tiny pit, lined with moist epithelium and surrounded with a rich supply of blood capillaries. At first these were simple pits, but higher in the scale, septa and cross septa develop, until the lung appears to be filled with tissue. The complicated pattern continues to add to the alveolar surface, until in mammals and birds it is comparatively enormous, so that the exchange of oxygen and carbon dioxide is ample. The lung pattern might be likened to the familiar pattern of the acinose gland, resembling a bunch of grapes, which divided and subdivided to reach eventually the bird and mammal con-

dition. Along with this increase in the complexity, muscles, cartilage, connective tissue, and other materials follow. In the sac-like lungs of the early tetrapods, the bronchii extend to the anterior end of the lungs, but not into them at all; but, as septa and cross septa add to the complexity of the cavity, the bronchii must extend farther into the lungs. The reptilian bronchii are rather short and simple, although in the crocodiles the bronchii begin to make quite an extension into the lungs. Birds have a complicated bronchial structure, and the maximum is reached in the mammals, where the bronchus, with its cartilaginous supports, forms a finely subdivided tree, the smaller ends or twigs not having cartilaginous supports but being finely subdivided to reach the alveoli. One of the best pictures of the mammalian lung is obtained by injecting the bronchian tree, arteries and veins, with celluloid of different colors, and corroding away the tissues with acid. This gives a negative of the lung structure that is very instructive. Lungs dried under pressure of compressed air show the outside form in a very pleasing manner. These must be thoroughly dried and poisoned to keep away insect and mammalian pests. The lung is supplied with an extensive series of lymphatic vessels that extend to every part of the lung tissue. The innervation is through the pulmonary branches of vagus and the autonomic system, which together form plexuses that supply the lung. The arteries from the aorta extend into the lung tissue and supply the nourishment needed.

Amphibian Lungs. — The lungs of the Amphibia are quite variable, being sac-like in the forms that remain in water and having mainly hydrostatic function, but becoming more alveolar in those that spend most of their time on land (Fig. 288). The lung of *Necturus* is thin, poorly vascularized, and mainly hydrostatic in function. A *Necturus* with a total length of 270 mm. has lungs 77 mm. in length and of small diameter. *Ambystoma*, with a total length of 150 mm., has a lung 35 mm. long, of much better quality, and with good vascularity. *Amphiuma* with a length of 770 mm. has a right lung 550 mm. in length and a left 410 mm. In both *Siren* and *Amphiuma*, the lung is approximately as long as the body cavity. The lung of the Anura, in contrast to those of the Urodela, is not greatly elongated, is of much better quality, with more alveolar spaces, and with a better blood supply. The anurans are also better equipped to force the air into the lungs by a more highly developed skeletal and muscular structures. The hairy frog of Africa, with its hair-like development on the epidermis, has added this to its cutaneous system, according to Noble. No amphibian has lungs large enough to carry on all the necessary work of respiration, and the cutaneous system supplements this work and gives the additional surface necessary.

Reptile Lungs. — The lungs of reptiles are of a higher type than those of the amphibians. Because of the presence of scales and plates, a cutaneous system would be worthless to most reptiles, except to a few with smooth skins that live in the water (Figs. 190, 191, 192, 298). There is a tendency for the lungs of the lower reptiles to have a more or less barren region at the posterior end, similar to that of the lower amphibians. In chameleons, this is prolonged into small airsacs, somewhat like those of birds. The breathing action is improved by a better development of the accessory structures such as the larynx, a trachea with cartilaginous rings, ribs and a body musculature that aid in respiration, a better nasal passage, and a better musculature of the mouth and throat. The lungs are free in the body cavity, as in amphibians, and there are no pleural sacs. The simplest lungs are those of lizards and snakes (Fig. 300), in which the septa are not highly specialized and the bronchial tree not developed, since it just connects with the lungs and does not extend down into them. These lower reptile lungs are not much of an improvement over those of the best amphibians. Those of snakes are greatly elongated, and the development of septa is slight. Snakes (Fig. 190) usually have the left lung reduced or vestigial (Figs. 191 and 192). The best reptile lungs are those of the turtles and crocodiles, and these approach the mammalian types in the fine sub-division of the septa and the bronchial tree. The lungs of reptiles have a much better blood supply, since there is little possibility of assistance from a cutaneous source, the blood supply approaching that of the mammal in quantity. It is highly probable that some of the ancient reptiles such as the pterodactyls and dinosaurs had lungs of a very advanced type.
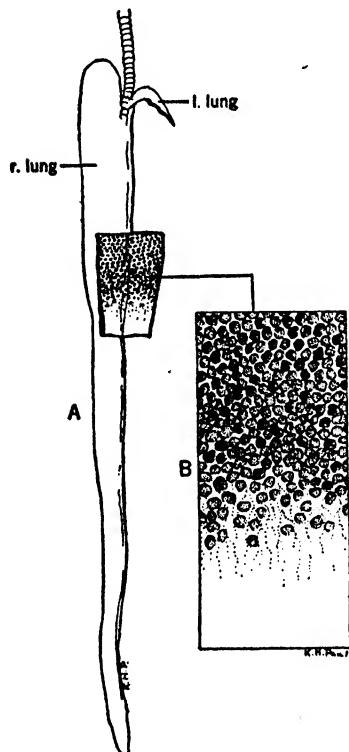
FIG. 190. A, lung of a Natrix, anterior aspect; B, enlarged portion of lung to show alveolar structure.

Bird Lungs. — Birds have an extremely efficient respiratory system (Fig. 310), since their high-tension lives demand a large amount of oxygen. The lungs are filled with septa and appear sponge-like in section. The
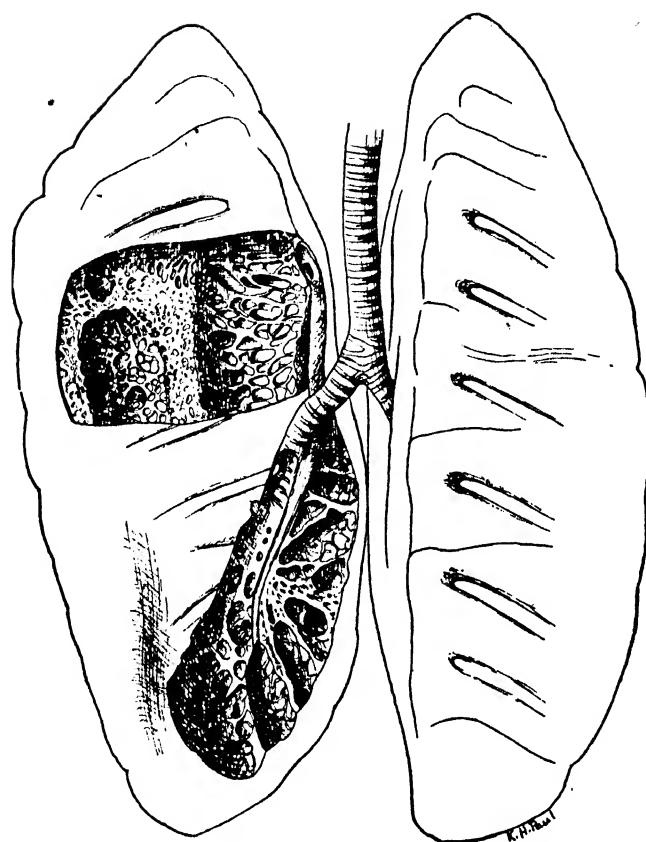
FIG. 191.   Lung of Mississippi alligator, posterior view to show organization of the septa, and distribution of the bronchii.   After H. Marcus.
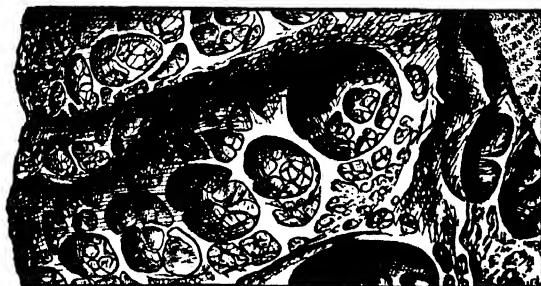
FIG. 192.   Section of lung of snapping turtle, *Chelydra serpentina*, to show finer structure.

respiratory area per pound of body weight is consequently very high. Two features stand out distinctly in the lungs of birds: the development of the airsacs, and the peculiar division of the bronchial tubes. The accessory airsacs which connect the lungs with practically all parts of the body are supplied with arterial blood and appear to have other functions than those connected with respiration. These sacs, usually six in number, are connected with the skeleton, thus making it pneumatic. The pneumaticity varies greatly within the class, but generally the best fliers have the best development of these sacs. The connection with the skeleton is sufficient to permit breathing through one of the long bones, if the trachea is tied. The bronchii bifurcate and enter the lung, forming secondary bronchii, which in turn give off a series of tubes that retain about the same diameter throughout. The bronchii and some of the tubes open into the airsacs, so that there are no blind passages in the
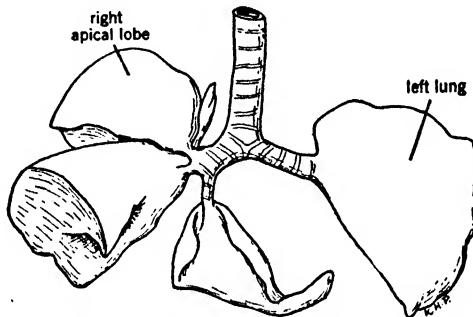
FIG. 193. Lung of Echidna. After H. Marcus.

lungs of birds. The airsacs make the body pneumatic, preserve heat, lessen the friction between flight muscles, and assist in respiration by making possible a complete change of air in the lungs at every breath. The diaphragm is incomplete and of small value in changing the air in the lungs, but the skeletal parts are in such close connection with the lungs and accessory sacs that any movement of the body assists in moving the air.

Mammalian Lungs. — The lungs of mammals (Figs. 193, 194, 195, 196, 197, 321), like those of birds, are sponge-like in appearance. They are enclosed in pleural sacs and are suspended in the pleural cavity through the attached vessels, the heart, and the mediastinum. They are separated from the rest of the body cavity by the dome-shaped diaphragm. Inhalation and exhalation are carried on by means of movements of the ribs, intercostal muscles, sternum, and the muscular diaphragm, by which the capacity of the chest cavity is increased and diminished. The abdominal muscles also play a prominent part in the
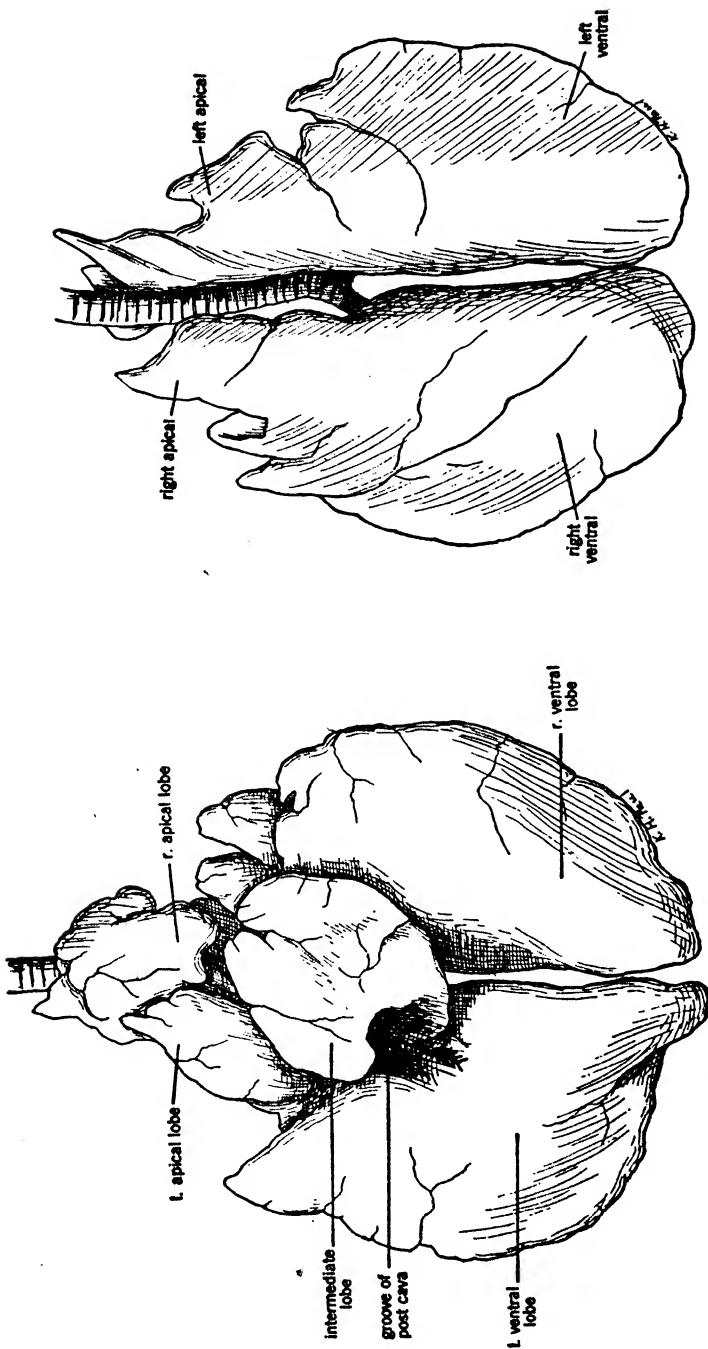
FIG. 194. Lung of an ox, posterior aspect; anterior aspect.

process.   The air is conducted to the lungs through the nasal cavity and pharynx, to the glottis.   The trachea, extending down into the lungs, bifurcates before entering.   On entering the lungs, the bronchii, usually two in number, divide and subdivide until they become small tubes, still protected by rings of cartilage.   The bronchioles or final conducting tubules are without cartilage.   The bronchioles connect with the infundibula and the areas where the alveoli are to do their work.   In this
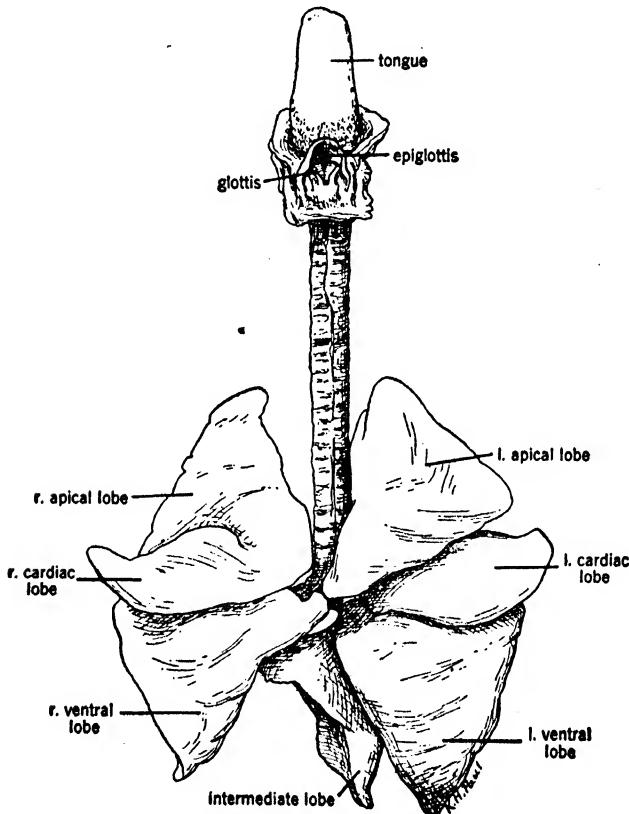
Fig. 195.   Lung of domestic cat.   Anterior aspect.

way, every part of the mammalian lung is connected with the bronchial tree.   The cartilage of the bronchial system becomes progressively less organized, until in the final divisions the cartilages are slightly connected plates.   The alveoli of the infundibula are lined with moist epithelium, laced with capillaries, and through these the interchange of gases takes place.   The respiratory centers of the brain control the lung action,

keeping the carbon dioxide at a definite level. The lungs are extremely elastic and can be expanded several times their normal size without breaking. There is a considerable amount of cartilage, practically all of which is in connection with the bronchii, and smooth muscles which wrap around them forming a latticework. The pulmonary arteries, coursing along the bronchii, extend to the limits of the lung and supply the blood that is to extend into the alveoli. Coursing along the bronchii also are corresponding veins, which pick up the blood after it has been through the alveoli and return it to the heart. As mentioned before, the
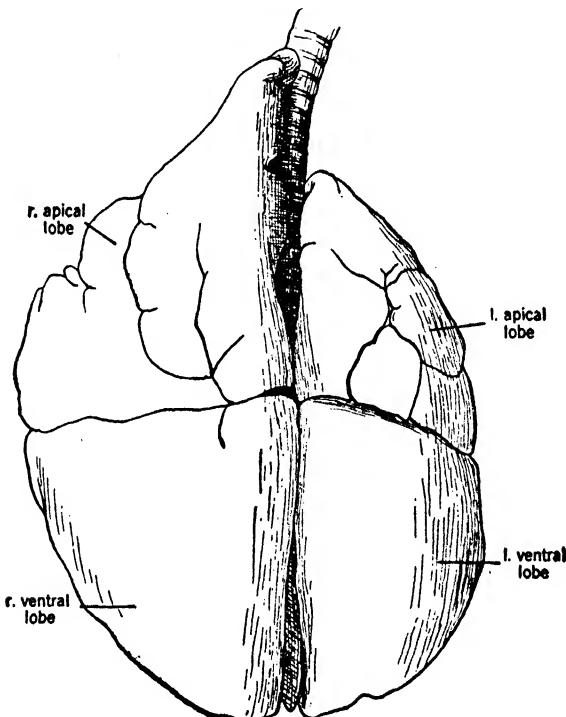
FIG. 196. Lung of a dog. Anterior aspect.

main innervation is through the pulmonary branch of the vagus and the branches from the autonomic system.

There is considerable variation in the lungs of mammals, since the formation of the lobes may be somewhat different in the same species. Since the heart is on the left side, there is always a difference between the right and left lobes, both in number and size.
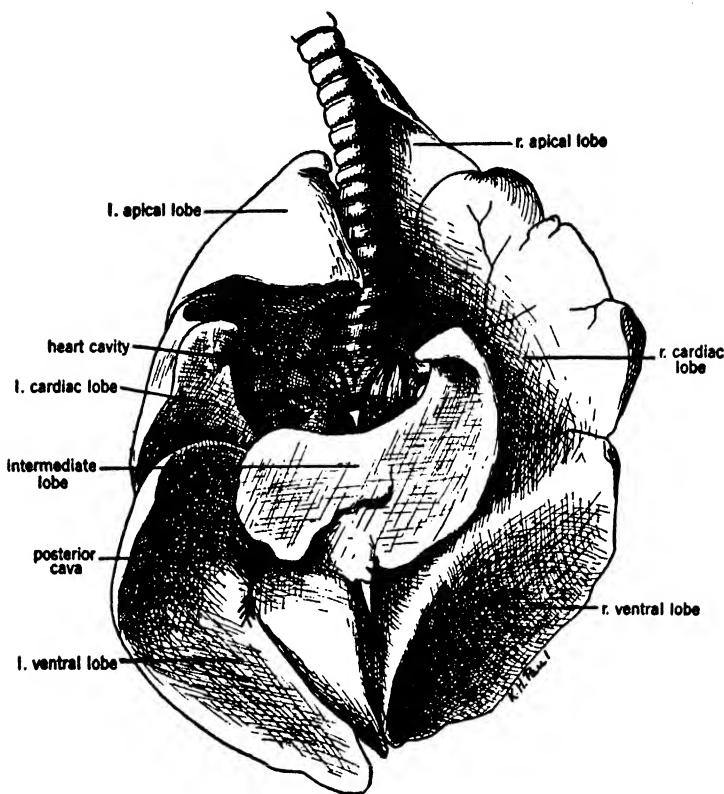
Fig. 197. Lung of a dog. Posterior aspect.

Résumé

Respiration, as discussed in this chapter, is the process of supplying oxygen from the air or water to the blood stream and releasing carbon dioxide. This exchange of gases takes place through moist membranes in the gills of fishes; in the gills, lungs, and skin of amphibians; and in the lungs of reptiles, birds, and mammals. Gill slits are formed from endodermal pouches of the pharynx, which become attached to the ectodermal body wall and break through to the exterior. The number of gill slits decreases above the fishes. Gills are formed in connection with the gill slits and are strengthened by the branchial or visceral arches and other parts of the skeleton. The lamellae, or thin plates on the surface of the gills, contain capillaries, which conduct the blood close to the external surface for the exchange of gases. Airsacs are usually hydrostatic structures in fishes, but in some groups they retain an open duct to the digestive tube and act as accessory organs of respiration. Lungs are membranous sacs, either simple or highly subdivided by partitions, in which gases are exchanged under the same conditions

as in gills.   The trachea changes from a soft-walled tube in fishes to one ringed with cartilages in higher vertebrates.   The larynx, at first with a mere slit-like opening from the pharynx to the trachea, eventually is reinforced with cartilages and becomes a sound-producing organ.   The accessory sacs connected with the lungs in birds and some reptiles are filled with air and assist in respiration.   The mammalian lung is separated from the rest of the body cavity by a diaphragm, which cooperates with the muscles of the ribs, sternum, and abdomen in inhalation and exhalation.   The lungs may be simple or made up of several lobes and are usually asymmetrical.

CHAPTER IX

NERVOUS SYSTEM

The nervous system is a highly specialized part of the animal body, simple or complex as the type of the organism demands. It begins to develop at an early stage in the embryo, from the outer germ layer, the ectoderm. From an outside position in primitive forms, the system has retreated inward as the complexity of the animals increased, until in the higher forms the main parts are well buried under bone and muscle and, hence, better protected.

The nervous system is built up by intensifying and adding to the possibilities that already exist in protoplasm, the material from which life is made. First, protoplasm is sensitive, being able to recognize changed or variable conditions; second, it is able to transmit sensations from one part of the mass to another — conductivity; third, it is able to make a response to this stimulation by a correlated action of the parts. By the specialization of these qualities and by adding a large number of parts, the highest nervous manifestations known are possible.

Neurons. — The working units of the nervous system are specialized cells, the neurons. Some neurons are modified into neuroglia which act only as supporting cells. Each neuron consists of a cell body, which has a nucleus concerned with nutrition of the cell, and two or more processes, or fibers, which extend out from this body and come in contact with similar processes of other cells, thus connecting the different parts by synapses. The processes are of two kinds: the dendrites, which receive the sensation; and the neurites, or axons, which transmit the impulse to the next connection. The microscopic structure of the cell body shows fine fibrillae which are supposed to conduct the impulses through it. A stimulus, picked up by the dendrites, is transmitted through the cell body to the neurite and passed to the next cell or to other cells. It is assumed that sensations always go through a cell in the same direction. The synapses are assumed to be mere temporary contacts that can be withdrawn or remade at any time. The insulation of the nerve fibers is a covering called the myelin sheath, made up largely of fat and giving the fiber a white appearance. It in turn is surrounded by a cellular layer, the neurilemma. At intervals the myelin layer is pinched in, followed by the neurilemma, which approaches closely to the fibers, forming the nodes of Ranvier.

The fibers from the individual nerve cells are collected together to form nerves, and in this way distant parts are connected with the central system and with adjacent structures. Some of these cell fibers are quite long, reaching from the spinal cord to the tips of the limbs, a distance of several feet. The fibers are of two kinds: the sensory fibers, which lead the stimuli in to the central system; and the motor fibers, which take stimuli out to the different parts of the organism. The processes from the neurons grow out from the central system, the brain and spinal cord, and extend to all parts of the animal. Ganglia are formed by the withdrawal of neurons from the central system in the embryological stages.

Reflex Arcs. — The most primitive type of the nervous system consists only of effectors, which cause organs or structures to act. This simple system is found only in the lowest invertebrates. The second type results from the addition of specialized receptors, which receive

the tail in fishes and gradually shortening in the higher forms until it hardly reaches to the sacrum in mammals. It is in a protective tube of cartilage or bone and is surrounded with the same protective sheaths as the brain — the dura mater, arachnoid layer, and pia mater. In cross-section it is seen to have an inner region of gray matter, consisting of nerve cells and fibers, somewhat in the shape of an H or a butterfly; and outside of this is a region of white matter composed of nerve fibers, which give it its white color (Fig. 212).

The white matter of the cord, consisting of nerve fibers, is divided by the gray matter into three regions or funiculi, a dorsal, lateral, and ventral. Each region, in turn, has bundles of fibers of varying size and function. The fasciculi, or mixed fibers of different origins and terminations, make up these regions. In general, the fibers of the dorsal funiculus are sensory, those of the lateral funiculus both sensory and motor, and those of the ventral funiculus motor. The sensory or ingoing columns are increasing in size, as they are augmented by additional fibers from the successive spinal nerves; the outgoing or motor tracts become reduced in size for they are sending fibers out to the spinal nerves. The dorsal funiculus contains bundles of fibers going to the different areas of the brain, a large tract, to the cerebellum, and others extend on to the anterior part of the brain. The lateral funiculus has both sensory and motor fasculi, the large rubrospinal taking impulses from the cerebellum and other parts of the brain back down the spinal cord, and the spinothalamic connecting the cord with the thalamus. The ventral funiculus is a motor pathway, and through it, the large pyramidal, thalamic, and other tracts reach the limits of the body.

The gray matter (Fig. 212) of the cord is made up of nerve cells, fibers, and neuroglia or supporting cells. It is in the form of a letter H, and the lumen of the cord is in the middle of the cross bar. The pattern of the gray matter varies with the region of the cord. The gray matter is divided into anterior, middle, and posterior columns, the gray matter extending to the periphery of the cord where the fibers come in from the dorsal root, and ventrally where the fibers leave to form the motor roots. The organization of the gray matter is rather complicated, since its functions are so varied. It has reflex connections for impulses that enter the cord and that are sent back to the body for reflex action; it connects the segments of the body by forming collaterals that join two or more segments together; it is the origin of the fibers for the motor roots and receives sensory fibers from the dorsal roots. It is the distributing and sorting structure for both ingoing and incoming fibers, supplies collaterals for connecting different levels of the cord, supplies cells concerned in reflex action of the body, and supplies commissures

that enable fibers to cross and recross, so that body movements can be synchronized in any way necessary.

Spinal Nerves. — The spinal nerves are arranged metamerically in pairs. Each spinal nerve has a dorsal sensory root with a ganglion and a ventral motor root with no ganglion. This division of function of the two roots was worked out by Bell and is called Bell's law. The spinal nerves extend out through spaces between vertebrae. Each nerve immediately divides into three branches: a dorsal ramus to the dorsal body wall, a ventral ramus to the ventral body wall, and a visceral ramus to the viscera and autonomic system. All the rami may contain visceral fibers, but the visceral ramus is made up mainly of this type (Fig. 212).

Brain

In common with the spinal cord, the brain is formed by an invagination of the ectoderm. Phylogenetically, the brain represents an external system removed to the interior of the body. It is a product of cephalization, with the mouth and its sense organs as a focusing point. As in the cord, the ventral part of the brain is essentially motor, and the dorsal part, of later development, is sensory. The dorsal parts represent a superstructure added to the primitive brain as the occasion demanded. The needs of land life made great differences in the suprasegmental brain. The working structures of the brain consist of many types of neurons in different combinations, small groups called nuclei and large groups or areas of associated neurons, specialized or general in function. A series of ventricles and thin membranes, or choroid plexuses, supply some of the metabolic needs of the brain. Since the brain is a bilateral structure, many cross connections are needed to insure synchronism of action. The larger and better organized cross-fiber tracts are called commissures. Some functions of the brain are localized so that it may be divided into areas that are in control of certain definite parts of the body.

Relative Size of the Brain. — There is a rapid increase in the size of the brain as the animal scale is ascended and as land life is assumed. The following table (from Weber after Dubois) shows the ratio of brain weight to body weight for a few of the mammals:

Elephant	*Elephas indicus*	1 : 560
Dolphin	*Tursiops tursio*	1 : 432
Whale	*Globicephalus melas*	1 : 400
Man	*Homo sapiens*	1 : 45+
Marmoset monkey	*Mystax midas*	1 : 26
Spider monkey	*Ateles ater*	1 : 15

It is interesting to note that the brain of man is neither the largest in actual size nor the largest in proportional weight. Both the whales and the elephants surpass man in the actual size of the brain, and the marmoset and spider monkeys both surpass man in its proportionate size.

Divisions of the Brain. — The divisions of the brain are formed by difference in function and by a difference in the growths of the parts concerned. The lowest type of brain, that of *Amphioxus*, consists of a single vesicle, which may be called the archencephalon. The cyclo-
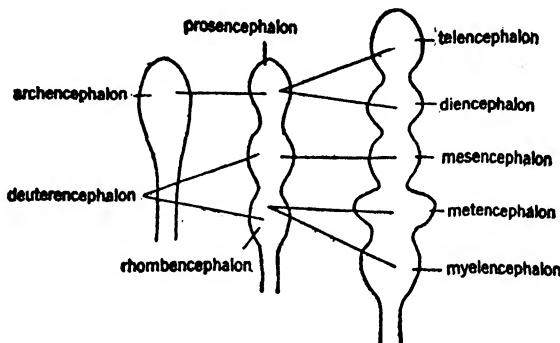
Fig. 198. Diagram showing origin of divisions of brain.

stomes develop this into a prosencephalon and another region, the deuterencephalon, which later divides into two lobes, the mesencephalon and rhombencephalon, and in this way the three-lobed brain is formed. In the fishes the anterior and posterior lobes each divide again, thus forming the five-lobed brain (Figs. 198, 203). The following diagram shows the development of parts of the brain.

Amphioxus	Hypothetical intermediate	Cyclostome	Shark
Archencephalon —	Archencephalon	— Prosencephalon	{ Telencephalon / Diencephalon
	Deuterencephalon —	Mesencephalon	— Mesencephalon
		Rhombencephalon	{ Metencephalon / Myelencephalon

Flexures. — In the formation of the brain, the more rapid growth of some parts bends the tube so that flexures are made in certain areas (Fig. 199), consisting of an apical or parietal, a nuchal or cervical, and a pontile. These flexures straighten out in fishes, so that the brain is much elongated. In reptiles, birds, and mammals these flexures are retained, so that the brain, though much enlarged, is relatively short and the brain case is round.

Ventricles. — A series of cavities (Fig. 200) extend through the brain to aid in the metabolism of the structure. They are filled with lymph and usually are penetrated by the telea choroidea or choroid plexuses, (Fig. 203), thin membranous sheets filled with capillaries. In the telencephalon there are two lateral ventricles. They are not well differentiated in the lower fishes since this region is not divided into two complete lobes, but in the higher fishes the division is more complete and the two ventricles are evident. Each opens into the third ventricle by an interventricular foramen, the foramen of Monro (Figs. 200, 211). The third ventricle is usually narrow, and a large choroid plexus extends down into it and through the interventricular openings into the lateral ventricles. The cavity is further restricted by the soft commis-
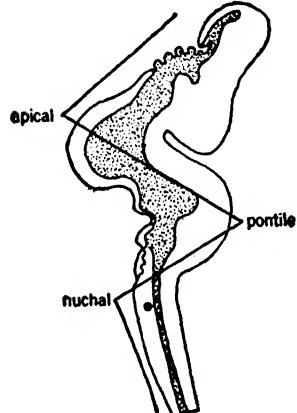
FIG. 199. Brain of snake embryo (Natrix) showing flexures.
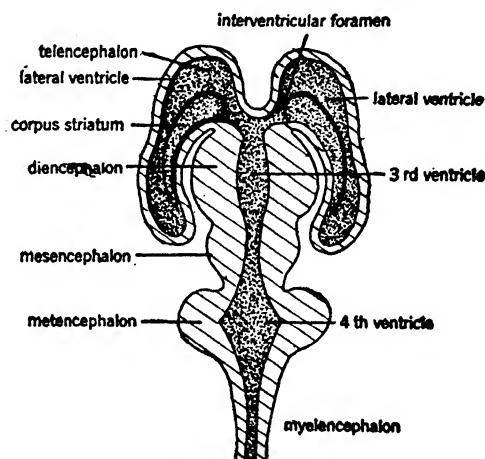
FIG. 200. Brain ventricles. After Villiger.

sure (Fig. 211) which extends across the ventricle. The cavity of the mesencephalon is large in the lower vertebrates and connected with the epicoels of the optic lobes, but in the higher animals it becomes a small tube connecting the third and fourth ventricles. The cavity of the metencephalon, the metacoel (Fig. 203), is also found only in the lower forms, for with the growth of the metencephalon it becomes completely obliterated. The fourth ventricle is the cavity of the myelencephalon. It is also covered with a choroid plexus. In higher animals this ventricle extends forward into the metencephalon.

Meninges. — The brain has the same coverings as the spinal cord. The dura mater is closely attached to the skull, forming a tough, smooth lining. The arachnoid layer is fibrous so that it supplies the insulation

from shocks. The inner layer, or pia mater, is closely in contact with the surface of the brain, extending down into the folds, and carrying with it the blood vessels of the surface of the brain for purposes of metabolism.

Medulla. — The medulla, or myelencephalon (Fig. 203), is very much like the spinal cord in structure but gradually increases in size anteriorly. Since the fourth ventricle is large and has a non-nervous covering, the nerve paths must converge at the sides of the fossa rhomboidalis to get around it and to reach the rest of the central system, thus making a decided swelling at the sides of the fossa. Some of the paths are conspicuous, being marked by evident ridges. The pyramids, a pair of large descending tracts, make large swollen cords on the ventral side of the medulla. On the dorsal side, a number of ridges posterior to the fossa show the ascending gracilis (clava) and the fasciculus cuneatus. Although the medulla is small in comparison to the rest of the brain, it is not so simple as it appears. The last six cranial nerves, starting with facialis, take their exit from its sides or ventral region. Laterally the olive, or olivary nucleus, shows very plainly. The corpus restiforme, or posterior peduncle, forms the connection with the cerebellum. The reflex centers regulating the secretion of saliva, gastric and pancreatic juices, movements of the digestive tube, heart, blood vessels, and organs of respiration are also in this region of the brain.

Metencephalon. — The metencephalon consists of two well-differentiated parts: the ventral region, which is a continuation of the brain stem; and the dorsal, or supra-segmental region, the cerebellum (Fig. 203). The ventral part is similar to the same region of the medulla. It contains the nuclei of cranial nerves V and VI in its dorsal wall, and its ventral side is encircled by the band-like pons (Fig. 210) in the mammals.

The cerebellum varies from a very small and insignificant region in the cyclostomes to the very prominent lobes of the higher vertebrates. Although an elaborate structure in the fishes, it is small in the amphibians (Fig. 205), and it gradually increases in size and complexity, reaching its highest development in the mammals. Its origin seems to have been in connection with the vestibular nerve, and it has developed in connection with the increased importance of equilibrium, both in water and in land life. Originally a median structure, it has increased in complexity by the outgrowth of accessory parts, the flocculi (Fig. 207) and paraflocculi of birds and reptiles, and finally the cerebellar lobes of mammals, which completely cover the original parts of the metencephalon. The surface is covered with sulci and gyri (Fig. 211), so that its area is very large. On the inside the tracts of fibers from the
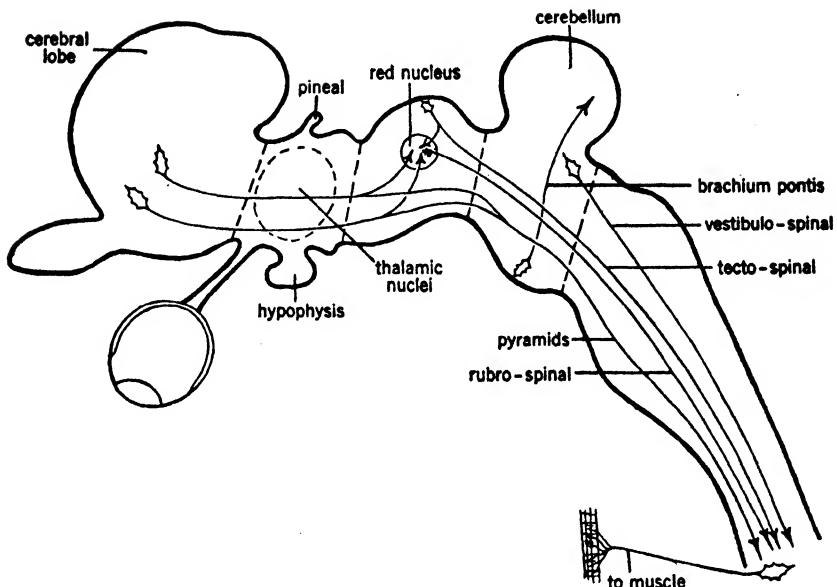
FIG. 201.   Diagrammatic representation of some of the main outgoing or motor tracts of the mammalian brain.
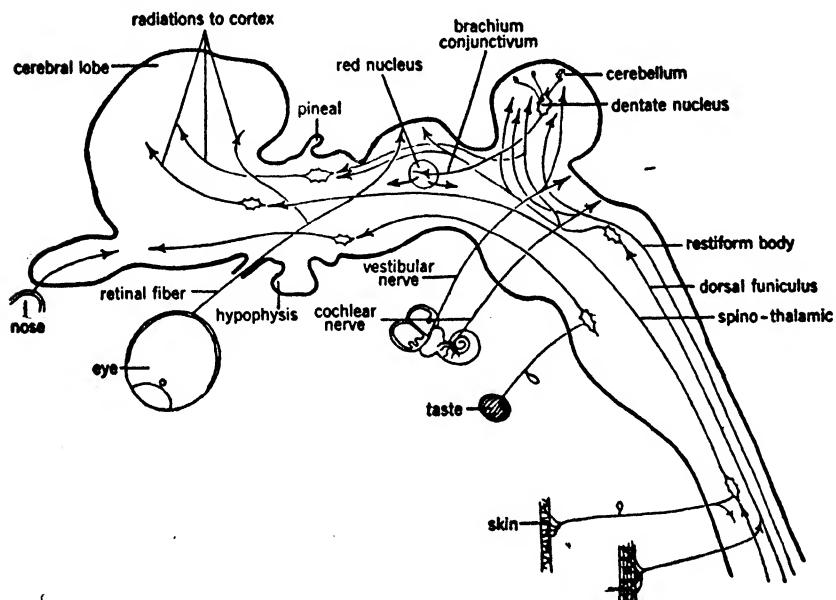
FIG. 202.   Diagrammatic representation of some of the main incoming or sensory tracts of the mammalian brain.

cortex converge and thus form the arbor vitae (Fig. 211). No nerves take their exit from the cerebellum, but it is rich in connections with other parts of the brain. The large dentate nucleus is the origin of the fibers extending anteriorly into the brain stem. The nucleus fastigii on each side receives axons from the vestibular nerve of the opposite side.

The arrangement of the cells of the cerebellar cortex is much the same for the whole structure, consisting of three layers, an outer, Purkinge, and an inner layer of nerve cells. The Purkinge cells have large, distinctive bodies, a number of much-branched dendrites, and an axone that connects with the anterior and pontile brachia.

The connections of the cerebellum with the rest of the brain are through the anterior peduncle (brachium conjunctivum), the posterior peduncle (restiform body), and the middle peduncle (brachium pontis). The pons forms a ventral band around the brain stem, connecting the two lobes of the cerebellum (Fig. 210).

The main function of the cerebellum is that of unconscious motor coordination and the preservation of muscular tonus, and it has numerous connections with the eyes, ears, muscles, joints, tendons, and other parts of the body. When it is removed the animal is unable to walk but may eventually recover to a limited extent, because other parts of the brain seem able to take over the function of maintaining the equilibrium, especially in mammals.

Mesencephalon. — The mesencephalon (Figs. 203, 205, 206, 208, 211), is a short, small region of the brain, connecting much larger parts. Its ventral part is the brain stem, and its dorsal part is made up of lobes, which do not change much in the different groups, except for the transverse splitting of the corpora bigemina (Figs. 205, 206, 207) to form the corpora quadrigemina (Figs. 209, 211) of the mammals. It is the original eye brain in fishes, but with the growth of the telencephalon its visual function becomes secondary in mammals, which have the main visual centers in the cortex of the cerebral lobes. The ventricle originally opened into the mesocoels of the optic lobes, but in the mammals it is small and tube-like and is called the iter (Fig. 211). Below the mammals the lobes (corpora bigemina) are usually large and conspicuous, and their importance to sight may be judged by their size. In mammals the posterior lobes of the corpora quadrigemina serve as a relay for auditory impulses. As would be expected, all the nerves connected with the eye muscles come from this division of the brain with the exception of the abducens, nerve VI, whose nucleus is in the metencephalon. The nuclei of nerves III and IV are in the ventral floor of the iter, and nerve II originally had its main connection from this

division. The red nucleus, a relay center which is partially in the diencephalon, receives fibers coming from the cerebellum through the anterior peduncle and sends them on to the cortex of the telencephalon.

Diencephalon. — The diencephalon (Fig. 203), which was formed from the posterior part of the prosencephalon, is a division in which there have been many changes. Its side wall, or thalamus (Fig. 209), is thickened and forms the main part of the brain stem through which most of the connecting tracts must pass to get to the anterior parts of the brain. In the lower fishes there are two epiphyseal bodies on the dorsal region of the diencephalon, a parietal body and a pineal body (Figs. 203, 209, 211), which probably represent an original pair of accessory eyes. In *Sphenodon* the pineal body (epiphysis) is structurally a direct eye, with a lens, retina, and nerve, and reaches the surface of the head through a foramen between the parietal bones. In birds and mammals it is covered by the other parts of the brain and becomes a gland of internal secretion. Anterior to these epiphyseal structures, the roof is covered by a choroid plexus. The pulvinar nucleus (Fig. 209) is a relay connecting the eye, the lateral geniculate, and the visual cortex of the telencephalon. In mammals the medial geniculate is connected with the inferior cerebral commissure, and the lateral geniculate is a relay between the eye and the cerebral cortex. The tuber cinereum (Figs. 208, 211) is a ventral extension of the diencephalon, terminating in a tube, the infundibulum. This in turn is connected with the hypophysis (Fig. 211), a diverticulum formed from the mouth (Rathke's pocket), which eventually closes again, leaving this tissue on the ventral side of the infundibulum. In the sharks the infundibulum becomes enlarged and folded to form the saccus vasculosus. The hypophysis, an endocrine gland that appears in all vertebrates, fits into a small depression in the floor of the brain case, the sella turcica. Two mammillary bodies (Fig. 211), in man about the size of peas, lie just posterior to the hypophysis and are concerned with the sense of smell. Anterior to the hypophysis, the chiasma (Fig. 210) of the optic nerves is a striking landmark. In the higher mammals, the optic nerves send most of their fibers through the lateral geniculates to the visual areas of the cerebral lobes. No nerve nuclei are found in the diencephalon.

The cavity of the diencephalon is the third ventricle (Figs. 203, 211), a very narrow, slit-like space, encroached upon by the growth of the walls or thalamic region. The soft commissure (Fig. 211) joins the walls in the higher animals, forming a bar-like connection across the ventricle. The third ventricle opens into the lateral ventricles by a pair of slit-like openings, the interventricular foramina (the foramina of Monro) (Fig. 211). The choroid plexus, extending down from the

roof, pushes forward so that a branch enters each lateral ventricle. The commissures are the superior (habenular) and the massa intermedia, (commissura mollis, soft commissure).

Telencephalon. — The anterior region of the original prosencephalon is the most variable of all the divisions (Fig. 203). Originally in fishes and lower vertebrates it was made up merely of partially divided lobes for the olfactory sense, but it becomes the most important center of volition and control, increasing in size until in man it covers the rest of the brain. The first change comes in the pallium (Fig. 203), which develops into two cerebral lobes with their millions of neurons, and in the higher forms the surface area is increased by sulci and gyri. To keep pace with the new anterior development, other parts of the brain are enlarged or changed. The changes require the enlargement of old
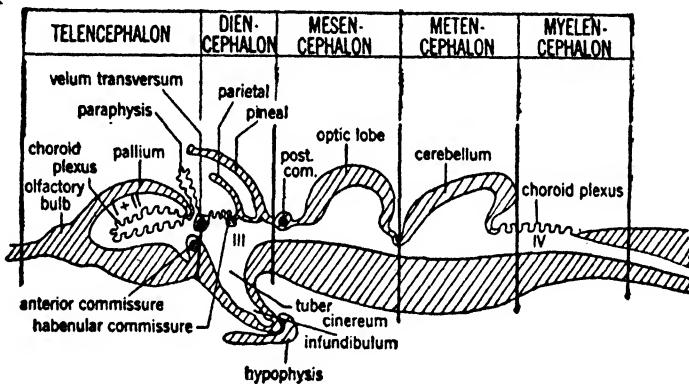
FIG. 203. Sagittal section of brain of shark. After Bütchli.

connections and the establishment of new cross-connections between the lobes. With the development of the cerebral lobes, the higher faculties are gradually acquired through the different classes of the vertebrates. In fishes there is little connection between the telencephalon and other parts of the brain, although there are some fiber tracts that extend to the basal region. Starting with the tetrapods, there is an increasing number of tracts connecting the telencephalon with the posterior regions of the brain and spinal cord; and in mammals, practically every part of the central nervous system has either direct or indirect connection, through relays with the cerebral hemispheres. In fishes the tracts of the telencephalon come from the nose to the olfactory lobe and have connections to the lateral walls of the diencephalon, but with the development of the pallium, the olfactory bulb is shifted to the ventral side, and becomes a very small part of the di-

vision. The basal region, the corpus striatum, assumes new importance and grows along with the pallium, assisting in making the required new connections with the other parts of the brain. It becomes enlarged and differentiated, and its neurons become localized for motor control. A new pathway leads from the walls of the diencephalon to the ventral region of the corpus striatum and thence to the cortex of the cerebral lobes. The fibers in this pathway pass through the thalamus and then through the caudate and lentiform nuclei. The cross-connections, or
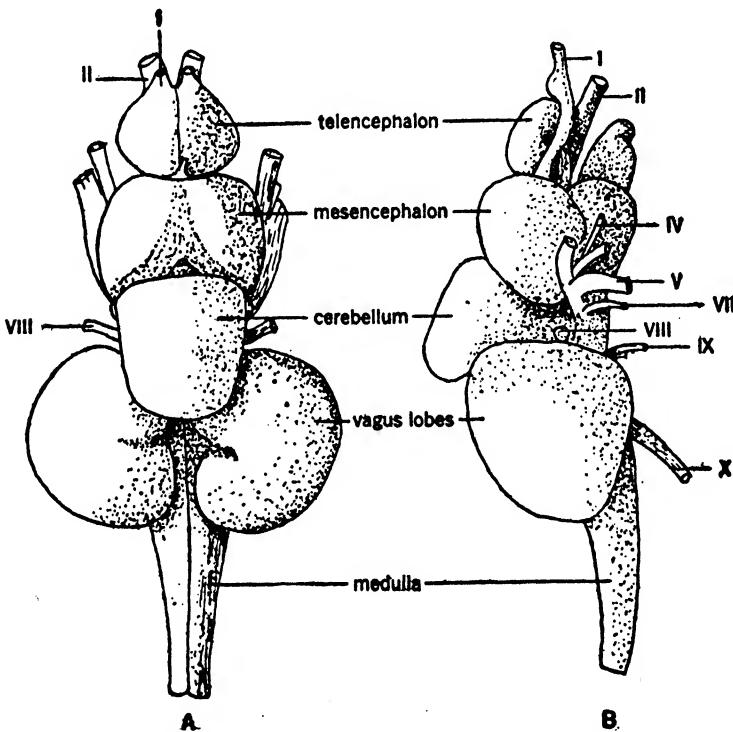
FIG. 204. Brain of teleost (Ictiobus) after Herrick. A, dorsal; B, lateral.

commissures, are increased with the development of the cortex. In addition to the original anterior commissure, which is in the lamina terminalis of the fishes, two extra commissures are formed: the pallial commissure, which splits to form the large corpus callosum (Figs. 209, 211), found in mammals above the monotremes; and the hippocampal commissure, which connects the hippocampal regions of the telencephalon and forms the pillars of the fornix. The corpus callosum serves the dorsal areas of the cortex.

The pathway from the spinal cord to the cortex is through the thal-

amus of the diencephalon, then through the internal capsule, and out to the cortex through the corona radiata. This contains both the afferent and efferent fibers. It is not developed to any extent in the lower forms but reaches its maximum development in the mammals. Through this new system all parts of the brain as well as all parts of the body are connected with the cortex. The cortex itself is made up of a thin layer of cells, a few millimeters thick, which entirely covers the cerebral lobes. The rest of the material of the lobes consists of the connecting fibers.

In the lower forms the surface of the telencephalon is smooth, but as the higher forms are approached there is a tendency for the formation of lobate structures through the unequal growth of some parts of the surface. In man each cerebral lobe may be subdivided into five lobes: the frontal, parietal, occipital, and temporal lobes, and a covered insula of Reil, which lies under the temporal lobe. These are marked off by fissures to form fairly natural divisions. There is a localization of function in parts of the cortex, relatively small areas being in control of definite functions, such as hearing, seeing, smelling, word perception, writing, and movements of parts of the body.

Cranial Nerves

The cranial nerves, which originate in the brain itself, are variable in number: eight pairs in the cyclostomes, ten in the fishes and amphibia, and twelve in the reptiles, birds, and mammals. The additional nerves of the brain series seem to have come from the inclusion of more of the spinal nerves within the brain case.

The problems presented by the cranial nerves are: first, what they represent; and, second, how they can be compared with spinal nerves. In protochordates and cyclostomes, nerves come off from the central system both dorsally and ventrally, those from the dorsal region with ganglia and those from the ventral side without, but the two do not unite as do the true spinal nerves of the higher vertebrates. It is assumed that the cranial nerves were of the same form originally, that the motor nerves are those that were ventral and unganglionated, and that the sensory nerves, with their ganglia, are comparable to dorsal spinal nerves. No cranial nerves have the typical form of spinal nerves.

The problem of the cranial nerves with the original head segmentation is still unsolved, since conclusions are still indefinite as to just what is represented in the head region. A study of the developing head and brain seems to indicate that from nine to thirteen segments are concerned in its formation, and with these the cranial nerves are associated.

Cranial nerves I, II, VIII, and probably the nervus terminalis are made up of sensory fibers only. Nerves IV and VI are purely motor. The rest, with the possible exception of nerve III, have mixed fibers. The only nerves leaving the head region and extending to the body are X and XI. Nerves IX, X, and XI form a group that belonged to the gill region in fishes and appear to be composite nerves in higher forms.

Nervus Terminalis, Number 0. — This small nerve is not included in the original numbering system because it was not discovered until long after the system had been established. Pinkus discovered it in the fish *Protopterus*, in 1895, and it has since been found to be practically constant throughout the vertebrates. It originates in the cerebral lobe, extends to the membrane of the nose, and is associated with the organ of Jacobson. Although not well understood, it is assumed to be sensory, and it is possibly a part of the olfactory tract and not an independent nerve.

Olfactory Nerve, I. — The olfactory nerve originates in the olfactory bulbs of the telencephalon and, extending to the nose, innervates the region of this organ in which the sense of smell is located. It is really a tract, since the neurons extend the length of the structure, and the olfactory nerves themselves are the small twigs that extend out from the end of this tract to the mucous membrane of the nose. (Fig. 210.)

Optic Nerve, II. — The nerve of sight, also a tract, originates in the roof of the mesencephalon, extends anteriorly and ventrally through the brain, and takes its exit from the ventral side of the diencephalon, just anterior to the hypophysis. In the lower forms the origin in the mesencephalon is constant, but in the higher forms there is a gradual modification, with more and more of the fibers leading to the optic centers of the cerebral cortex. At its exit, a chiasma is formed in which the fibers merely cross in the fishes but gradually intermingle in the higher forms, so that fibers from each eye are directed to both sides of the brain, thus giving binocular vision. The optic tract ends in the retina, the small twigs innervating the rods and cones. (Fig. 210.)

Oculomotor Nerve, III. — This nerve, which originates in the mesencephalon and takes its exit from the same structure, innervates the eye muscles, namely, the superior, inferior, and internal recti, the inferior oblique, and the ciliary muscle and process. It acts as a part of the parasympathetic system in the ciliary process. (Fig. 210.)

Trochlear Nerve, IV. — It originates in the mesencephalon, taking its exit from the dorsal side, and innervates the superior oblique muscle. (Fig. 209.)

Trigeminal Nerve, V. — The origin in the brain is from two nuclei that extend from the mesencephalon through to the medulla. One

nucleus is sensory and the other motor, making it evident that it is a combined nerve. The exit is from the side of the metencephalon in close connection with the exits of nerves VII and VIII.. It has three main branches. The ophthalmic branch has its own ganglion and probably represents a separate nerve. In fishes it is divided into the ophthalmicus superficialis to the region of the orbit and the ophthalmicus profundus to the region of the nose, but it is not divided in other vertebrates. The maxillary branch, coming from the Gasserian ganglion, innervates the maxilla and its teeth. The mandibular branch, which extends ventrally, innervates the mandible and its teeth and most of the muscles of mastication. It has several subdivisions, one of which serves the tongue and is called the lingual nerve in mammals. (Fig. 210.)

Abducens Nerve, VI. — This nerve has its origin in the anterior part of the myelencephalon and leaves the brain from the ventral side of this structure, innervating the external rectus muscle. This is the last of the eye-muscle nerves. (Fig. 210.)

Facialis Nerve, VII. — The facial nerve originates in the medulla, and its exit is from the side of this division. It serves a region in which there has been much shifting of parts and decided changes in function, so that there is a considerable difference between the fish and the tetrapod condition. In the lower animals this ganglionated nerve parallels the region innervated by nerve V but is concerned principally with the lateral-line structures, such as the ampullae of Lorenzini and the series of lateral-line canals on the heads of fishes and amphibians. In fishes there are branches innervating the different sensory canals of the head region, the membranes of the mouth, and some of the muscles of the branchial region. In the higher tetrapods, the elimination of the sensory canals causes the dorsal branches to disappear, but three branches are retained, the palatine, internal mandibular, and a part of the hyomandibular. The internal mandibular, or chorda tympani, takes a peculiar course through the middle ear before going to the tongue. Fibers from the chorda tympani form a part of the parasympathetic system in control of the salivary glands. In mammals the chief function of the facial nerve is to control the mimetic musculature. (Fig. 210.)

Auditory Nerve, VIII. — This nerve, while having its origin in the medulla, is always associated with the metencephalon and the cerebellar lobes. It takes its exit close to that of the facialis and also probably represents a part of the acustico-lateral line system. In the lower vertebrates it originates from a single nucleus, but in the higher vertebrates, with the development of the cochlea and the organ of Corti, there is a division of the nerve into two branches, each having its own

nucleus, one innervating the semicircular canals and the other innervating the cochlea. (Fig. 210.)

Glossopharyngeal Nerve, IX. — This is a segmental nerve of the first gill slit that originally had a pre- and a post-trematic branch. It originates in the medulla and, leaving the side of this structure, innervates the first gill slit in fishes and sends a branch to the palate, which joins the palatine branch of the facial nerve. In the mammals it innervates the pharyngeal region and a part of the tongue. It has the petrosal ganglion at its base.

Pneumogastric Nerve, X (Vagus). — Originally the pneumogastric, or vagus, was a part of the lateral-line system. It represents several joined nerves similar to the ninth. It leaves the side of the medulla by several roots, each originally having its own ganglion but later formed into a single mass. In fishes it supplies the second, third, fourth, and fifth gill arches with pre- and post-trematic branches and with a long lateral branch that extends posteriorly to supply the lateral-line organs. With the dropping out of the lateral line and gills, the pneumogastric becomes a nerve of the viscera, sending branches to the digestive, respiratory, and circulatory systems. The heart, lungs, and stomach are well forward in the lower forms so that they are within the region controlled by the original vagus nerve, and as these structures have retreated posteriorly in the body cavity in tetrapods the nerve has followed them. It is also connected with the autonomic system as a part of the parasympathetic control. (Fig. 210.)

Spinal Accessory Nerve, XI. — This nerve is found only in reptiles, birds, and mammals. It seems to be a part of the vagus that has become independent in mammals. The nucleus is in the medulla, and its exit is from the same structure. In the fishes it is a nerve of the cord and innervates the muscles of the segment posterior to the skull; in the mammals it innervates the trapezius and the sterno-cleido-mastoid muscles. (Fig. 210.)

Hypoglossal Nerve, XII. — The hypoglossal has its nucleus in the medulla and takes its exit from the side of this structure. Only in reptiles, birds, and mammals is it included within the brain case. In fishes it innervates the tongue region and parts of the mouth and may even send a branch to the pectoral fin, but in mammals it is restricted mainly to the muscles of the tongue. (Fig. 210.)

Peripheral Nerves

The peripheral system, together with its auxiliary, the autonomic system, furnishes the means of nerve distribution. The outlets from the spinal cord (Fig. 212) are through the metameric spinal nerves that

must send fibers to all the regions of the body. The origin of each fiber is in the ganglia which early in the embryo sends out fibers that are to form all the future connections with the body. On the dorso-lateral walls of the spinal cord, crests are developed into which the neurons migrate to form the sensory ganglia of the dorsal roots. Ventrally on the cord other fibers extend out, forming the ventral roots, but these are without ganglia, since their neurons are within the cord itself. The dorsal and ventral roots of each nerve join together and immediately subdivide into three branches, the dorsal, ventral, and visceral rami. From these branches fibers grow to all parts of the body. The fibers may be divided into four types: somatic sensory, visceral sensory, somatic motor, and visceral motor. The ends of the sensory fibers are in sense receptors in all parts of the body. The motor fibers in a similar manner must eventually reach the different regions where they end in muscles and other structures. The autonomic system, containing both sensory and motor fibers, which grow from the visceral rami, controls the viscera. In regions of the body where there is much activity, nerves from a number of sources become interlaced and closely connected by collector nerves, thus forming subsidiary control centers called plexuses.

Autonomic System

The autonomic system consists of a part of the peripheral nerves that have been somewhat isolated from the rest to form a subsystem for special work. It is formed mainly from neurons that have withdrawn from the ventral part of the spinal cord, and consists of ganglia and nerves with an organization similar to that of the main system, since it has receptors, adjustors, and effectors, but is not under conscious control. These nerves and ganglia of the autonomic system complete the machinery necessary to control such organs as the heart and lungs, which have a continual action; and the digestive system, in which non-striated muscles continue to work for a long period of time. All the movements initiated by this system are rather slow, in contrast to the fast action possible in the voluntary system.

The autonomic system is known only in the vertebrates, but it seems probable that their invertebrate ancestors used a part of their nervous system for a similar purpose. It is possible that some part of the invertebrate system has supplied the basis for its development in the vertebrates. However, these conjectures are highly questionable and do not answer the question of the origin of the autonomic system of vertebrates. Starting with the cyclostomes and fishes, there is a progressive development of the system that is much better known in the higher forms of vertebrates.

The system is often divided, for convenience, into the parasympathetic and sympathetic systems, the parasympathetic consisting of the fibers carried by cranial nerves III, VII, IX, and X and sacral nerves 2, 3, and 4. The oculomotor sends fibers to supply the ciliary muscles of the eye, the facial nerve sends fibers to the salivary and submaxillary glands, the glossopharyngeal to the otic ganglion, and the vagus to the viscera, including the heart, lungs, vasomotor system, bronchii, stomach, intestines, liver, pancreas, and kidney. The posterior part of the autonomic system connected with sacral nerves sends fibers to the colon, bladder, and urogenital organs. Fibers coming through these nerves are usually antagonistic to those of the sympathetic system, and this double innervation is continued to all parts of the body, one set of fibers starting an action and the other set stopping it.

The sympathetic part of the system consists of a chain of ganglia in the head, neck, and body that are connected with the visceral ramus of the spinal nerves through a gray and white branch. In the head region there is an irregular distribution of the ganglia, with no segmental arrangement. All these head ganglia are connected with the superior cervical ganglia and follow along the blood vessels, principally the carotid. The head ganglia consist of the ciliary which supplies the ciliary muscles of the iris; the sphenopalatine, which supplies the blood vessels of the lining of the nose; the otic, which supplies the muscles of the ear structures; and the submaxillary, which supplies the submaxillary and sublingual glands. The ganglia of the neck consists of a fairly large superior cervical and a smaller median and inferior cervical. These cervical ganglia are connected with the head ganglia, but also supply fibers to the body cavity, each sending a nerve to the heart and lungs. Starting with the first thoracic and ending with the fourth sacral, two chains of ganglia extend along the vertebral column, supplying the organs and structures of the body. These have a segmental arrangement, and there is a pair of ganglia for each spinal nerve in this series, each ganglion being connected with the cord by a gray and a white branch. In man this series consists of twenty-one ganglia. The system is extended out to form a network around the organs, with concentrations of nerve material where there is a great deal of action. With few exceptions (bone marrow and the substance of the brain) these fibers extend to every part of the body. Plexuses placed at centers of action consist of the cardiac, associated with the heart and lungs; the coeliac plexus of the digestive organs and associated structures; and the pelvic plexus connected with the urogenital organs and other structures of the posterior part of the body. The fibers of the autonomic system may be divided into two types, the pre- and post-ganglionic, the

preganglionic fibers originating from the cells within the central system, and the postganglionic fibers from the cells of the sympathetic system. The connection of these ganglia with the cord is through a white ramus, consisting of medullated fibers, and a gray ramus that consists of un-medullated fibers.

The chromaffin cells accompany the autonomic system in its with-drawal from the cord during embryonic development. These contain epinephrin, a substance important in animal life. The hormones from these cells make possible the explosive action of muscles. In higher animals, these cells are in the adrenal glands.
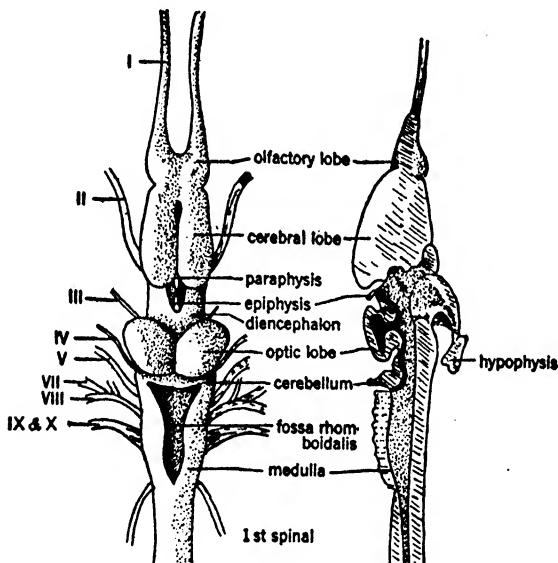
FIG. 205. Brain of frog (Rana). Dorsal and sagittal.

The Brain

There has been a gradual change in emphasis from the lowest verte-brates, in which the sense regions of the brain are large and prominent, to the highest vertebrates, in which the cerebral lobes are in complete control.

Brain of Amphioxus. — The brain of *Amphioxus* (Fig. 1), consisting of only one vesicle, is smaller than the adjacent parts of the spinal cord and has but a single ventricle. The neuropore remains open throughout the life of the animal. The posterior region perhaps represents what is to be the deuterencephalon. The sensory centers are problematical, since the animal has no eyes and nothing to indicate a sense similar to hearing

or equilibrium. The olfactory sense seems to be the most important.
Cranial nerves are present, but it is impossible to homologize them with
the nerves of the higher forms.   The spinal nerves have two roots,
which do not join as in the higher vertebrates.
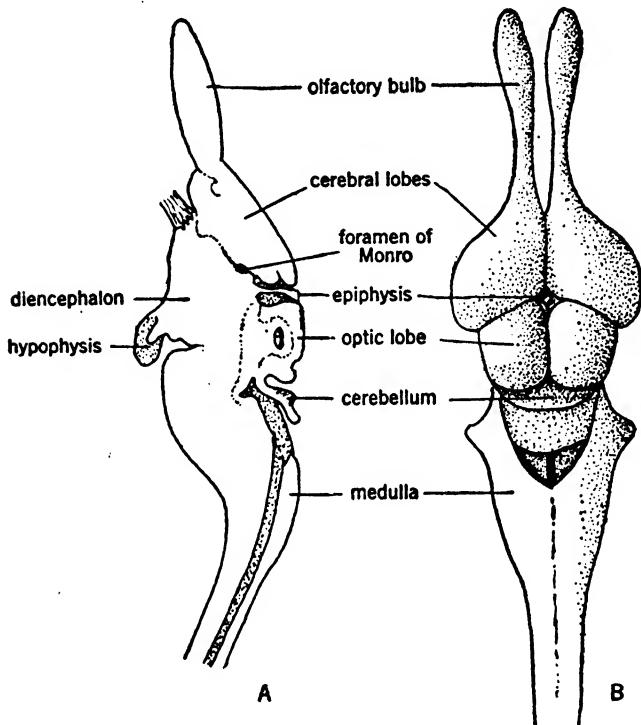
Fig. 206.   Brain of snake (Natrix).   A, sagittal section; B, dorsal.

Brain of Cyclostomes. — The brain of *Petromyzon* is that of a primi-
tive vertebrate, with three divisions, the pros-, mes-, and rhomb-
encephalon.   Since the senses are acute, the brain is assuming the fish
type, with the sense areas enlarged.   Four ventricles are present, al-
though that of the prosencephalon is only partially divided and is not
similar to that of the higher forms.   The olfactory and visual senses
have had a great influence on the brain, and their associated areas are
very prominent, but equilibrium is of less importance and its center is
small.   The cerebellum is a small band of nerve tissue across the an-
terior end of the fossa rhomboidalis.   Two small pineal structures
appear on the roof of the diencephalon, and the infundibulum projects
from the ventral side with its associated hypophysis.   The cyclostomes
have eight cranial nerves.

Brain of Fishes. — The brains of the fishes are quite variable within the class (Figs. 203, 204, 280). The brain of the shark is of a high type, that of the teleost is quite different in the regions stressed, and that of the Dipnoi is strongly suggestive of the brain of the amphibians. The proportionate amount of brain tissue is small in comparison to the body weight. The brain of the fish is largely a sense structure, with developments of nervous tissue for the regulation of smell, sight, and equilibrium. The roof of the telencephalon is not developed except in the Dipnoi, and the anterior part is not well connected with the rest of the brain. The olfactory lobes are always large and prominent, the eye lobes are out of proportion to the other parts, and the cerebellum is large and well developed. The pineal structure is prominent in the sharks, extending anteriorly to a small foramen in the chondrocranium; it is reduced in the teleosts, but it is well developed in the Dipnoi. The cerebellum seems to vary with the habits of the animals, being large in the good swimmers and small in others. Enormous vagus lobes develop in response to the sense of taste, as in the buffalo fish (*Ictiobus urus*). The forebrain of the Dipnoi resembles that of the amphibians in that the pallium is somewhat thickened and contains neurons. The fish brain is marked by a greatly enlarged corpus striatum. Fishes and amphibians have ten cranial nerves, the glossopharyngeal (IX) and the pneumogastric (X) having been added to the eight found in the lowest vertebrates.
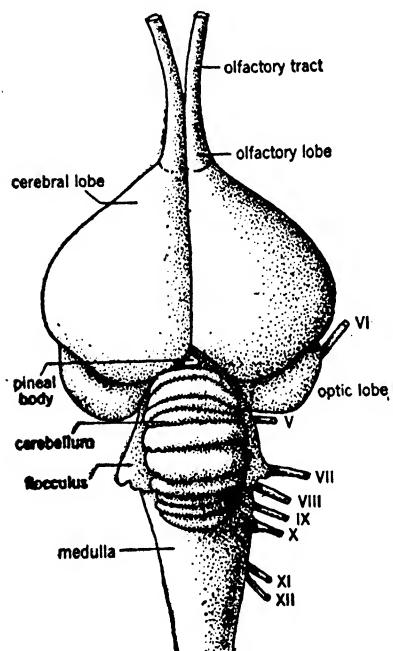
FIG. 207. Brain of chicken (Gallus). Dorsal.

Brain of Amphibia. — The brain of the amphibians (Figs. 205, 291) is quite distinctive in that the telencephalon is larger, with a greater development of the pallium and a reduction of the corpus striatum. The pallium is being invaded by neurons and is suggestive of what is to appear in the reptiles. The lobes of the telencephalon, as a rule, are distinct, although they are joined in the Anura. The cerebellum is small, but the optic lobes remain of large size, since there is no decrease in the use of the eyes. In the ancient Stegocephalia, the pineal structure

was very large, judging from the size of the parietal foramen, but in modern amphibians it is quite small.

Brain of Reptiles. — The brain of the reptiles (Figs. 206, 304, 305) is a decided step in advance over that of the amphibians, both in structure and in proportionate size. The most striking change is in the cerebral lobes, where the pallium is being invaded by nerve cells. With the increase in the cerebral lobes, there is a corresponding increase in the thickness of the thalamus, since more tracts must pass through to reach the anterior lobes. The pineal eye attains its best development in certain of the reptiles, being very prominent in *Sphenodon* and in most of the lizards. The sense structures are still large, but the emphasis is
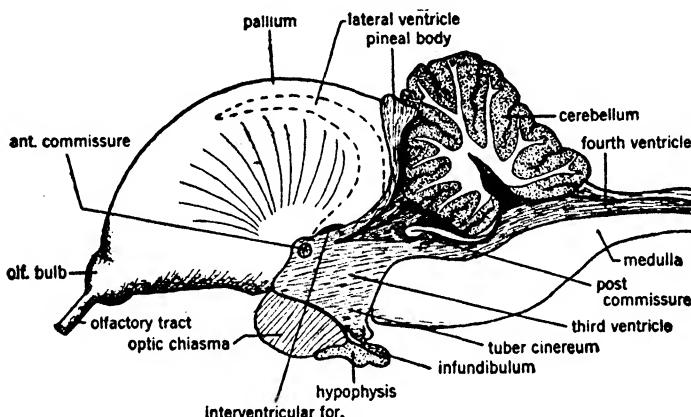
FIG. 208. Brain of chicken. Sagittal.

changing and the region connected with the sense of smell is gradually being reduced. The eye and ear retain their importance and have large brain centers. The cerebellum is rather simple but is increasing in size and, with the additional flocculi in Crocodilia and other forms, is considerably better than that of the amphibians. The infundibulum and hypophysis continue to be well developed. Two cranial nerves have been added, the spinal accessory (XI) and the hypoglossal (XII), making a total of thirteen if we count the nervus terminalis. This number is continued in the birds and mammals. Although the brain is much improved over amphibian conditions, by a large increase in the number of tracts and connections with the anterior part, the proportionate size is still quite small, since the brain of a 200-pound alligator weighs but a fraction of an ounce.

Brain of Birds. — In birds (Figs. 207, 208) there is a still further increase in the size of the cerebral lobes, but this is principally in the

enlargement of the corpus striatum, since the pallium is thin and poorly
developed. The sense of smell is reduced, with a corresponding de-
crease in the size of the olfactory lobes. The cerebral lobes overlap
the mid-region and extend posteriorly almost to the cerebellum, which
is still a median structure with large lateral flocculi but is decidedly
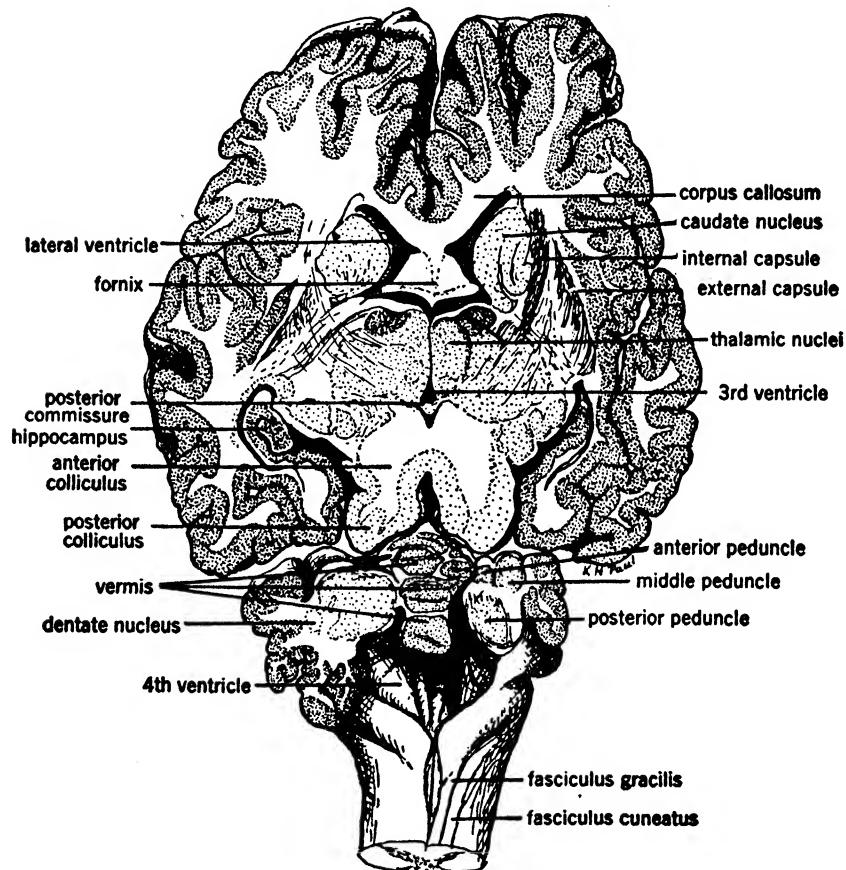
FIG. 209. Frontal section of sheep brain through posterior commissure and posterior
colliculus. Natural size.

larger than that of the reptiles. The optic lobes are large and are
forced out laterally by the cerebral overgrowth. There is an increase in
the connections of the several parts of the brain, corresponding to its
increased size. The olfactory bulbs are reduced to small structures at
the anterior end of the telencephalon. The pineal eye is small, not
reaching the skull roof, and the hypophysis is well developed.
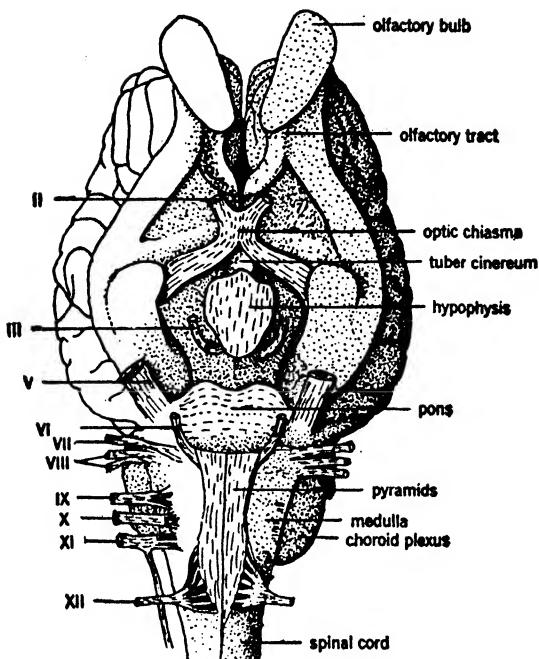
FIG. 210.   Brain of sheep.   Ventral.   After Sisson.
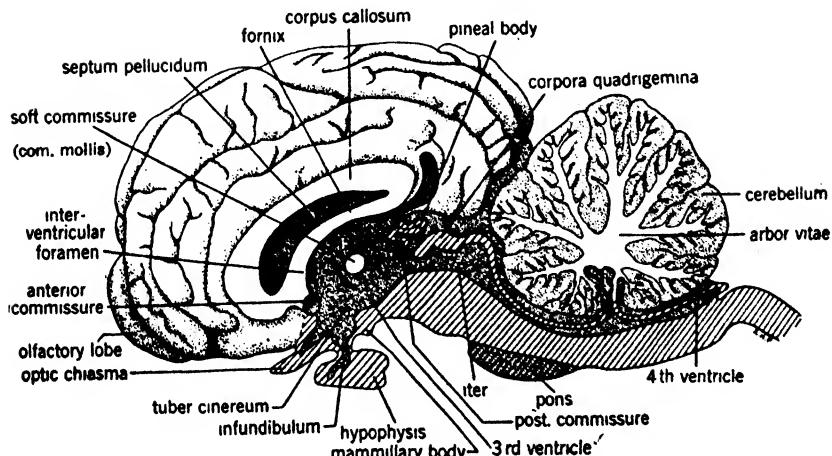
FIG. 211.   Sagittal section of mammal brain, diagrammatic.

Brain of Mammals. — The mammal brain is strikingly different from that of any of the lower forms, both in size and in structure (Figs. 209, 210, 211, 325, 326). Proportionately, it is much larger, and there is a difference in the relative development of the divisions. The cerebral lobes now become the predominating structure, and there has been an enormous increase in the number of tracts and interconnections necessary to make its functioning possible. The cerebral and cerebellar lobes are so enlarged that the other divisions seem small in comparison. The cerebral lobes are formed principally by the greatly thickened pallium with its increased mass of neurons. The surface is smooth in the lower mammals, but in the higher there is a tendency to increase
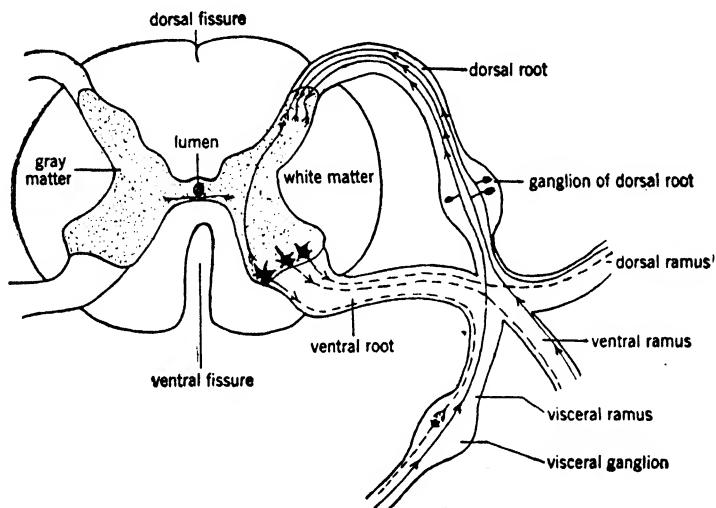
Fig. 212. Diagrammatic section of spinal cord with nerve roots and rami. After Plate.

the surface area of the cortex by folding and by the formation of sulci and gyri. The corpus callosum, a cross-connection between the cerebral lobes, appears in the higher mammals. The diencephalon remains small, and the pineal structure becomes a gland. The hypothalamus is well developed and the hypophysis is prominent. With the increase in the size of the cerebral lobes, the walls of the diencephalon are thickened in the thalamic region to accommodate the large number of tracts. The mesencephalon remains small, and the optic lobes lose their importance, since new optic centers are developed in the cortex of the cerebral lobes. The corpora bigemina of the lower forms divide transversely, forming the corpora quadrigemina of the mammals, but only the anterior pair are associated with sight. The cavity connecting the

third and fourth ventricles becomes reduced to a small tube, the iter. There is an increase in the complexity of the cerebellum by the addition of the cerebellar lobes and their cross-connections in the pons, a group of fibers extending around the ventral side of the brain stem, forming a prominent band in the higher mammals. Two other connections, the anterior peduncle (brachium conjunctivum) and the posterior peduncle (brachium restiforme), extend anteriorly and posteriorly from the cerebellar lobes.

Résumé

The nervous system is a complicated structure of correlating cells in which the general properties of protoplasm (sensitivity, conductivity, and correlation) are put to special uses for the control of the whole organism. The unit is the neuron, a nerve cell with a nucleus, an axon, and one or more dendrites. The connection between two nerve cells is a synapsis, where the ends of their processes are close enough together to permit an impulse to pass from one to the other. The simplest reflex is made up of a receptor, an effector, and an adjustor. The central nervous system consists of the brain and spinal cord, and the peripheral nervous system consists of the nerves and ganglia outside the central system. The brain was originally a concentration of nerve cells that developed in response to the needs of the sense organs associated with the mouth. Flexures are formed because parts of the brain grow more rapidly than others. Three membranes cover the brain: the outer, or dura mater; the medial, or arachnoid layer; and the inner, or pia mater. The vertebrate brain consists of five divisions: telencephalon, diencephalon, mesencephalon, metencephalon, and myelencephalon. Fishes and amphibians have ten pairs of cranial nerves, and most of the amniotes have twelve. (The nervus terminalis is not included in the original numbering of cranial nerves.) The vagus, or tenth cranial nerve, sends branches into the body cavity. The spinal cord, which is the main pathway of nerve fibers between the brain and other parts of the body, is enclosed in a canal of cartilage or bone and has the same protective coverings as the brain. The cord itself is divided into an inner region that contains nerve cells and an outer region that is made up entirely of nerve fibers. Pairs of spinal nerves extend from the cord to parts of the body. The autonomic system, a part of the peripheral system, has its own ganglia and nerves, which regulate the processes of digestion, respiration, and other activities that are continued over long periods of time and are not under conscious control. The chromaffin cells of the autonomic system are concerned in the formation of the adrenal glands. Some structures of the brain are constant throughout the vertebrates, but many changes take place in the several divisions of the brain and in their interrelations as the evolutionary scale is ascended; these changes consist in the addition of new structures, tracts, and commissures, the increase in size and importance of some parts and decrease of others, the development of new functions, and the enlargement of the brain mass in proportion to body weight.

CHAPTER X

SENSE ORGANS

Animal life is protected by its sense organs, and its central system is kept informed of outside occurrences by sets of receptors that have become specialized to deal with particular stimuli. Land animals have retained many of the receptors common to water life, but they have also added new ones necessary for their adjustment to a land habitat.

The sense organs consist of a series of simple and complex receptors originally developed from ectodermal cells. The primitive receptors end in the skin, but these may be withdrawn within the body wall and
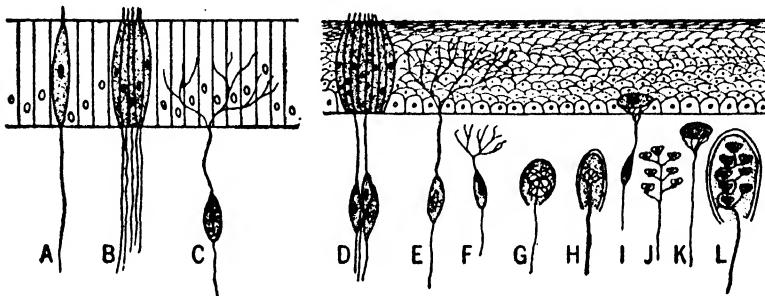
Fig. 213. Diagram of epidermal sense organs in chordates. After L. Plate. A–C, primitive sense cells of acraniates; D–L, sense cells of vertebrates. A, single sense cell; B, sense bud; C, free nerve endings in epidermis; D, sense bud; E, free nerve ending in epidermis; F, free nerve ending in corium; G, sense cells with nerve fiber wound in a capsule; H, encapsulated sense cell; I, epithelial tactile cell; J, group of tactile cells in corium with no capsule; K, tactile cell in corium; L, encapsulated group of tactile cells in corium.

may acquire numerous accessory parts. The simplest end organ is a nerve itself which spreads out in a network close to the surface, among the epidermal cells of the skin. Many specialized cells are found in the skin, for the perception of heat, cold, pressure, etc.; and specialized end organs of sense cells are found in the lateral line, eye, nose, ear, and taste buds. Interiorly, special cells for receiving stimuli are found in the muscles, joints, and tendons, and in the digestive organs for the perception of hunger, thirst, pain, etc. No animals, however, are known to have developed sense receptors for protection against certain radiations, such as X-rays, which have harmful effects on the body.

It seems probable that all specialized cells have developed from unspecialized touch receptors, or nerves that were generalized in their reception of stimuli of various types, chiefly by contact. Early in the history of the vertebrates, and before that time in the invertebrates, these cells became specialized. Several developments were necessary to existence, especially in those senses connected with food-getting. Thus taste and smell were developed early in animal life, with sight following closely. The organs of equilibrium developed in the invertebrates and were probably present in the first vertebrates. The temperature receptors were also important, since many aquatic animals have narrow temperature limits. The sense cells of the lateral line and the ear mechanism are probably related, since their functions are somewhat similar. In the adaptations to land life, the olfactory organs were modified, the eye was changed to a longer range of activities, and hearing was added to the sense of equilibrium.

Simple Sense Cells

Besides the highly specialized and organized sense structures, such as those for sight and hearing, single sense cells and small groups of sense cells (Fig. 214) are scattered over the surface and in the deeper
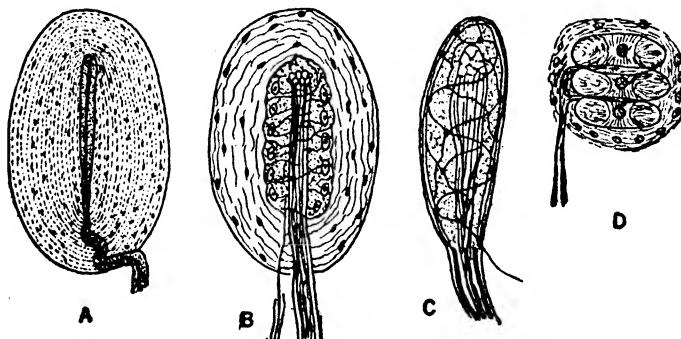
Fig. 214. Sense corpuscles of different types. A, Pacinian corpuscle from the mesentery of a cat (after Bohm, Davidoff, and Huber); B, Herbst's corpuscle from the tongue of a duck (after Plate); C, Krausse's corpuscle (after Bütchli); D, Grandry's corpuscle (after Bütchli).

parts of the body that are associated with other sensations. These may consist of plain nerve endings or of rather complicated special end organs, or corpuscles. Specialized receptors are found in the skin, especially on parts of the body that are modified for special uses, as the bills of some birds, the nose of the mole, the snout of the pig, etc.;

and also in the conjunctiva of the eye, in the taste buds, and in the cells of the lateral line (Fig. 215). Other receptors may be merely naked nerve endings among the epidermal cells. Inside the body, in tendons, joints, bones, teeth, and mesenteries, a second series of receptors function to provide for the needs of each region.

Neuromasts. — Some rather simple sense organs, called neuromasts, are found in the skin of cyclostomes, fishes, and water-living amphibians. Each of these epidermal sense organs consists of a few sensory cells connected with nerve fibers and protected by a number of non-nervous supporting cells (Fig. 215). They may be single, or a number of them may combine to form a series. Typically they are found in regular lines near each eye (suborbital, supraorbital, and infraorbital lines) and in a lateral line continuing along each side of the body to the tail region. They may sink into the skin and form ampullae, grooves, or canals, but
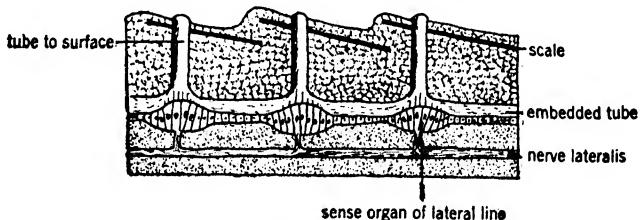
FIG. 215. Lateral line, diagrammatic. Modified from Kingsley.

each neuromast has its individual opening. The ampullae of Lorenzini, found in sharks, are in clusters close to the lateral-line organs and have the same innervation. The vesicles of Savi are found in some elasmobranchs, on the head and around the electrical organs. These ampullae and vesicles are filled with a clear jelly and are called slime organs. Their function is probably to register changes in pressure. The origin of the lateral-line system and the associated slime organs is from the dorso-lateral placode of the embryo, and the auditory pit originates from this same structure. This placode elongates, both anteriorly and posteriorly, and supplies the material for the canals on the head and lateral line in fishes and amphibians. The innervation is very characteristic and is constant in animals with these structures. The cranial nerve facialis (No. VII) is the one most closely associated with the canals on the head; the glossopharyngeus (No. IX) and the vagus (No. X) supply the lateral line with a nerve (lateralis of vagus) extending along the whole length of the body. This system and its nerves are completely lost in the land animals (Fig. 215).

Organs of Taste

The sense of taste is limited to testing materials that are sour, sweet, bitter, and salty. It is important for food-finding in the lower forms and for food-testing in the higher. The sense buds are skin organs, very similar to neuromasts in their structure, and they function only in moisture. The sense cells are contained in flask-shaped structures with sensory hairs projecting out of the flasks.

Taste buds are scattered along the side of the body, from the head to the tail, in many fishes. Since land animals have no need of taste cells except in the mouth, the buds become confined to the tongue, the lips, the circumvallate and foliate papillae, and parts of the throat. The innervation of the taste buds is generally by the glossopharyngeal nerve (No. IX), but there is some variation.

Olfactory Organs

Smell is one of the most primitive, as well as one of the most important, of the primary senses. The nose is situated anterior to the mouth, and innervated by the olfactory nerve and nervus terminalis. In the early vertebrates the anterior part of the brain is concerned almost entirely with the innervation of this structure. In fishes the rhinencephalon is relatively large, but in amphibians, reptiles, and birds, it gradually becomes reduced, and in mammals it is completely overshadowed by the great overgrowth of the cerebral hemispheres. The sense of smell was developed primarily for a water habitat, and the organs were perfectly adapted to this medium, but with the change to land life the nose retained its efficiency by connecting itself with the respiratory system so as to insure a constant sampling of the air, and thus was enabled to function in air as well as it did in the water. The cells for receiving the sensation are close to the surface and are the original neurons, since their bases are continued as fibers of the olfactory nerve (tract). Smell and taste are similar, but whereas the sense of taste is much restricted in its scope the sense of smell is almost unlimited in its powers of discrimination. The detection of odors in the air is a great source of protection to land animals, both in guarding them from their enemies and in helping them to find food. The testing of food is also carried on by this sense.

The olfactory organ is a paired structure in all vertebrates but the cyclostomes, in which it is single. The nose arises from epidermal placodes that are invaginated and drawn in to form shallow pouches, which in most fishes have no connection with the mouth. An oro-nasal

groove is formed in the rays, and the dipnoans have a tube connecting it with the mouth. In Amphibia the internal nares open into the mouth at its anterior end; in Reptilia a secondary shelf begins to drive the internal nares to the posterior. In Crocodilia and Mammalia this shelf drives the nares far back by the formation of a hard palate, a secondary structure built up by the palatine and maxillary bones.
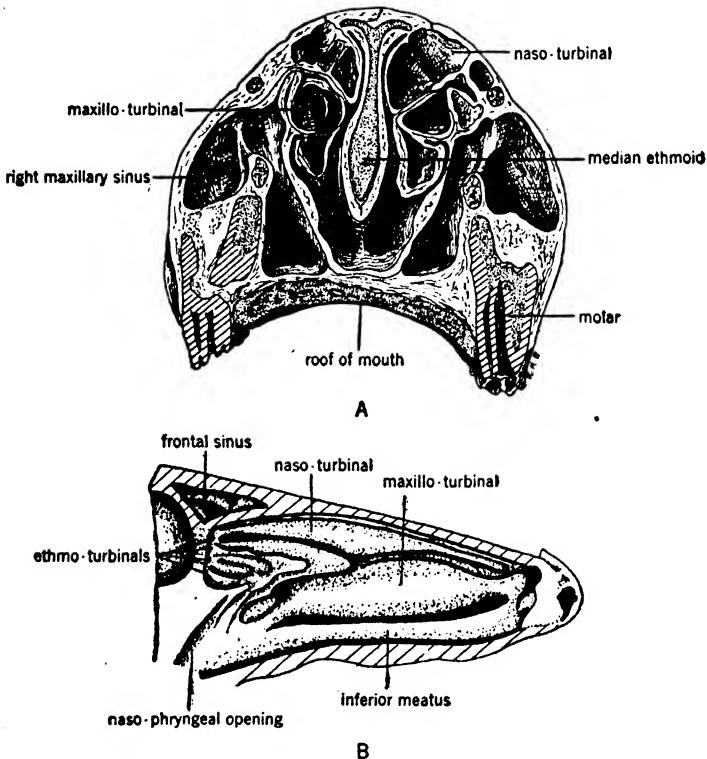
Fig. 216. A, cross-section of nose of a cow (original); B, sagittal section of a calf nose. After Weber.

Nose in Cyclostomes. — The cyclostomes have two olfactory nerves, which indicate that in all probability the original structure was paired. The nasal sac is close to the hypophysis, and the short tube that extends from the sac to its opening on the top of the head (between the eyes) also extends ventrally to the hypophysis, thus connecting it with the outside. In development the pit forming the hypophysis and nasal pit are close together but not identical. Later the two pits deepen and are gradually drawn into the skull on the ventral side, and finally, the growth of the enormous lip forces the depression to the dorsal side of the head.

Nose in Fishes. — The nose of the fishes has the form of a pit that is not connected with the mouth except in rays and lung-fishes. This olfactory pit is approached by openings of several types, indicating that there is a need for both an inlet and an outlet. *Acanthias* has a · flap that divides the opening, making it double. Some fishes have anterior and posterior openings, which are very helpful in getting the current across the sensitive membranes. The pit of *Acanthias* is enclosed in cartilage to form a thin-walled capsule. The olfactory nerve enters the capsule and spreads over the membrane, thus forming an olfactory surface. This inner membrane is thrown into folds attached to the periphery of the capsule and anchored by a septum. The folds are secondarily folded again thus giving additional area to the surface innervated by the olfactory nerve.

Nose in Amphibians. — The amphibians, as they became air-breathers, required some changes in the olfactory system, especially a connection between the nose and the mouth. This connection, by means of a tube entering the mouth or the pharynx, is retained in all the higher vertebrates. Surrounding the capsules are cartilaginous pouches as in the fishes. The external nares in the Anura close after the air is taken in, so that the air is forced into the lungs by the action of the throat muscles. The internal nares are small and just posterior to the dental ridge in the Anura. The tear duct and Jacobson's organ make their first appearance in the amphibians.

Nose in Reptilia. — The reptilian nose (Fig. 293 *A*) is a stage in advance of the amphibians, having additional parts and being better adapted to land life. The development of the accessory foldings starts with the reptiles, by the development of a bony conch on the ventral and lateral walls of the nasal passage. The internal nares open in the roof of the mouth. There is a division of the chamber into two parts, an anterior respiratory and a posterior olfactory portion. The tear gland discharges into the narial passage by a small duct. Jacobson's organ is well developed in most reptiles and is especially prominent in the lizards.

Nose in Birds. — The olfactory organs of birds (Figs. 314, 315) resemble in most respects those of the reptiles, although the conch is generally more complicated, forming a scroll. There is the same division of the nasal tube into a respiratory and an olfactory chamber. The interior nares open into single or double slits in the roof of the mouth and may be divided by a septum. The sense of smell is fairly well developed in some birds, but in general it is their weakest sense, since their sight and hearing are so much more acute.

Nose in Mammals. — The mammals have the greatest use for the sense of smell and have the most specialized nose found in the vertebrates. Scrolls, or conchae, develop on the sides of the narial cavity, thus increasing the surface exposed to the air. The lower anterior part is the respiratory chamber, used to warm and wash the air coming through on its way to the lungs. The upper posterior part of the passage is devoted to the olfactory sense, and the nerves of the olfactory tract reach the areas of smell through the cribiform plate.

The bony elements developed are the naso-, maxillo-, and ethmo-turbinals. These elements may be greatly subdivided and developed from the nasals, maxillae, and ethmoids. A number of sinuses, extending into the frontals, maxillae, and sphenoid, may develop in connection with the nose. The sinuses may be lined with olfactory mucous membrane in those animals with the highest development of the sense of smell, but in other animals they may have nothing at all to do with this sense (Fig. 216).

Jacobson's organ, which originates in amphibians from a small specialized portion of the nasal cavity, is in direct connection with the nose in mammals. In reptiles it is quite complex and has a duct of its own connecting with the mouth. It appears to be an accessory organ of smell. Certain mammals, such as the monotremes, marsupials, edentates, ungulates, and rodents, have a well-developed Jacobson's organ with an opening into the mouth through the incisive foramen. In man and other primates, the organ develops in the young but is lost in the adult, although the foramen incisivum persists as a vestige.

The external nose is practically a mammalian characteristic, and it is subject to many variations. A median plate-like cartilage supports the structure and at the same time renders it flexible, while the inner framework formed by the turbinals makes the organ effective. The specialization of the nose to form additional sense structures appears in moles and shrews, where it is tactile in addition to its usual function. Greatly extended noses are found in ungulates and in the elephants, with the formation of a trunk that becomes a prehensile organ.

The Ear

The ear serves in two very different ways, as an organ of equilibrium and as an organ of hearing.

Starting with the cyclostomes, all vertebrates have organs of equilibrium in which one or more canals are present. These canals continue throughout the vertebrates, always three in number in the fishes and the higher classes. They are set so as to detect variations of position in

any direction, since two of them are perpendicular and one horizontal. The canals are filled with a liquid, endolymph, in which float the otoliths, small crystals of calcium carbonate. Each of the canals is enlarged at one end, to form an ampulla (Fig. 217 *B*, 228), in which there is a sensory patch, or crista acustica, covered with hair-like projections from the receptors. Any change in the position of the body causes movement of the endolymph and otoliths, which strike the sensory hairs in the cristae acusticae. The sensation thus originating is transmitted through the fibers of the auditory nerve tract to the medulla and thence to the cerebellum, a part of the brain primarily concerned in equilibrium.

The part of the ear concerned in hearing has little or no differentiation in the cyclostomes but begins its development in the fishes, by the addition of accessory parts and by the formation of the cochlear branch of the auditory nerve. This development is associated with a number of
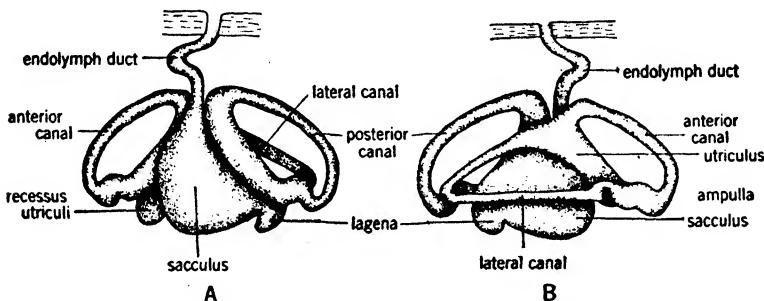
Fig. 217. Membranous ear of Squalus acanthias. A, mesial of right ear; B, lateral of right ear. After Retzius.

important changes in which the canals and utriculus become slightly separated from the sacculus and the beginning cochlea. This separation becomes more marked as the differentiation progresses in the vertebrates. The middle ear, with its two drums and a plunger, the stapes, appears first in the amphibians.

Development starts with an auditory placode, which becomes invaginated and finally drawn into the head in the region of the first gill cleft. This invagination forms a pit that opens to the outside and is retained in the sharks as the endolymphatic dûct (Fig. 217). This vesicle develops ridges that separate off, form a lumen, and develop into the semicircular canals. The utriculus, sacculus, and lagena are parts of the primitive ear of the lower forms, the utriculus being the body of the sac from which the canals were originally pinched off, while the rest of the vesicle develops into a sacculus and a second prolongation, the lagena, which is to become the cochlea of the higher mammals
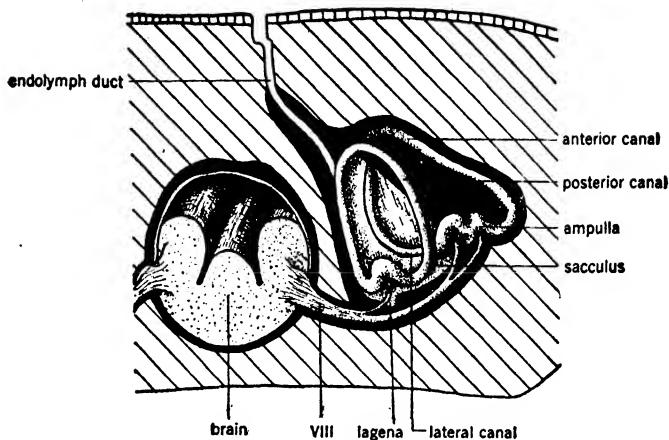
FIG. 218. Ear of shark as seen from the posterior.
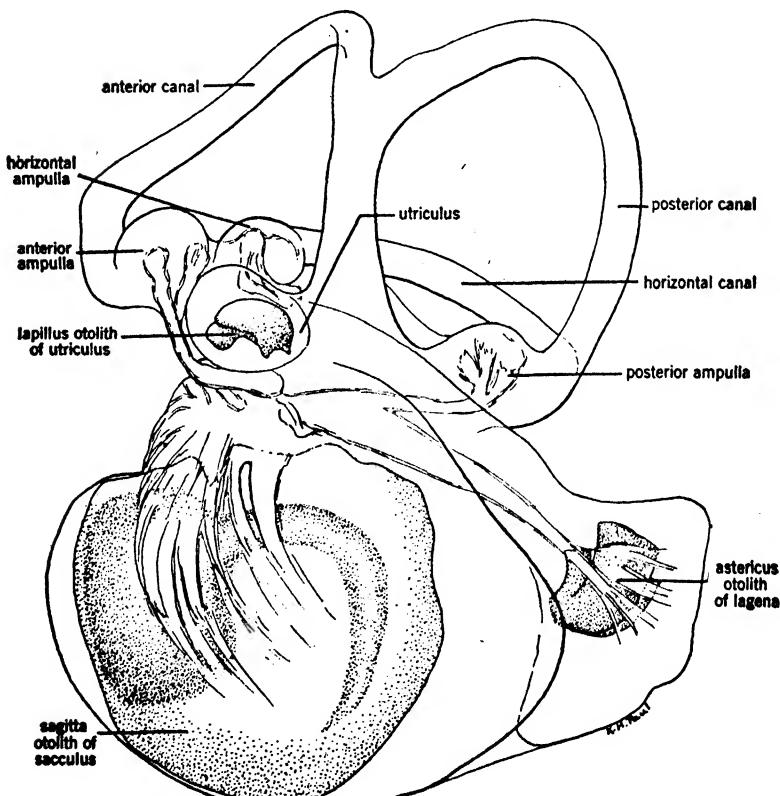
FIG. 219. Membranous right ear, mesial aspect, of the drum, ·
Aplodonitus grunniens.

(Fig. 217 *A*, *B*). The whole mechanism is very small and condensed, as it must be to find protection in the walls of the skull.

In fishes nothing but the inner ear is developed, and since equilibrium is its main function, the mechanism suffices for their needs. The receptors consist of the cristae acusticae (Fig. 228) in the ampullae, and the maculae acusticae on the other parts. In many fishes the otoliths become quite large and are called ear-stones (Figs. 219, 282). Some of the bony fishes have a tube connecting the airsac and the ear. The Ostariophysi have the Weberian apparatus consisting of a chain of bones that connect the airsac with the ear and probably register the air pressure of the sac (Fig. 181 *A*).

The ear of the amphibian (Figs. 220, 221) is a land structure with accessory parts that make it able to function in air. The middle ear,
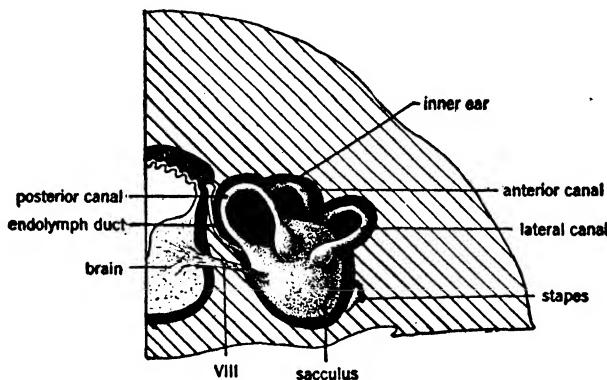
FIG. 220.   The ear of Ambystoma as seen from the posterior.

an additional chamber, is formed from the first gill slit and retains an opening into the pharynx through the Eustachian tube, or tuba auditiva. The stapes (Figs. 221, 222 *A*, *B*), which developed from the hyomandibular bone of the fish, acts as a plunger connecting the inner ear with the outer wall of the middle ear. In the Anura this connection is by means of a conspicuous disc, or drum. The stapes of the Amphibia consists of a basal plate, which fits into the foramen vestibuli, and a rod, the columella or plectrum (Fig. 221). The lagena is slightly longer than in the fishes.

The external auditory meatus is added in reptiles (Fig. 223), except the snakes. The greatest additional development comes in the lagena, which is elongated and curved, and in the membrana basilaris, which replaces the papillae lagenae. The lagena of the higher reptiles begins to have the characters of the mammalian structure, with an organ of Corti of a rather primitive type in the alligator. The lagena has a
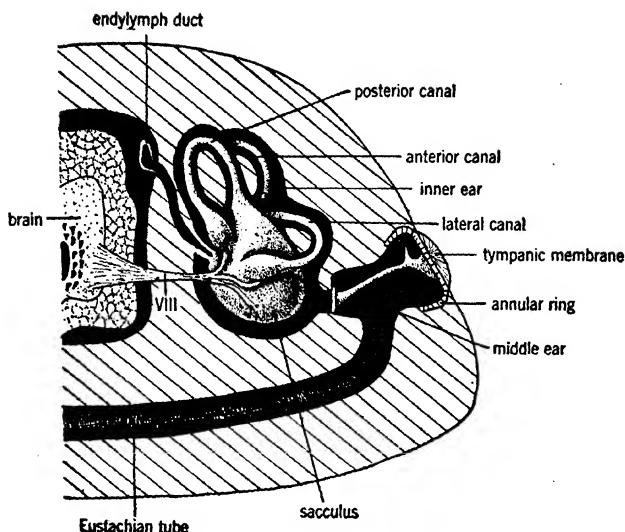
FIG. 221. Ear of frog as seen from the posterior.
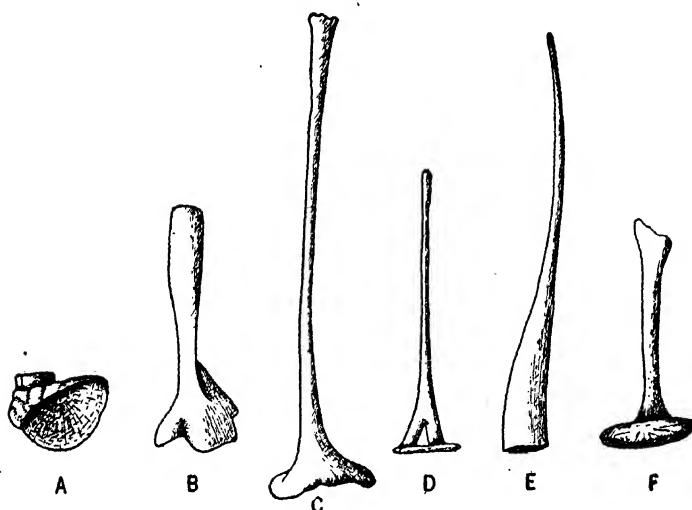
FIG. 222. Types of the columella auris. A, Necturus; B, frog (Rana catesbiana); C, turtle (Chelydra serpentina): D, alligator; E, sea-turtle (Thalassochelys); E, duck (Anas).

basilar membrane throughout its length, and by attaching itself at each side to the wall of its cavity it forms three ducts: a dorsal duct, the scala vestibuli; a median duct, the scala media; and a ventral duct, the scala tympani (Figs. 222 *C*, *D*, *E*, 227).

The ears of birds (Fig. 224) show but little improvement over the reptilian conditions. There is a greater elongation and specialization of the lagena, making it more like the mammalian cochlea. The Eustachian tubes join and open into the pharynx by a single duct (Fig. 224).

Mammals have the highest type of ear (Fig. 225), with three ossicles, the stapes, incus, and malleus. The lagena is specialized into the cochlea with its highly developed organ of Corti.
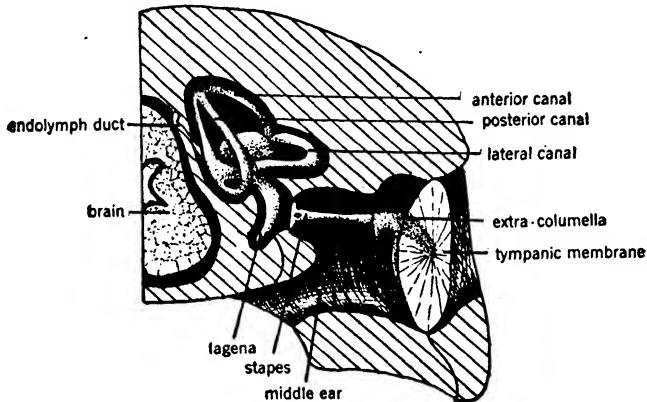
FIG. 223.   Ear of reptile as seen from the posterior.

Inner Ear of Mammals. — The semicircular canals (Fig. 230) of the mammals remain much as in the reptiles but are more firmly encased in very hard bone, the ivory-like periotic. The separation of the canals and the utriculus from the sacculus and the cochlea becomes more pronounced, and there is only a small duct connecting them (Fig. 230 *A*, *B*). The membranous ear (Fig. 230 *B*) is filled with endolymph and is surrounded by the perilymph, which transmits sound waves to the inner ear by the connection through the stapes. The endolymph and perilymph ducts have connections with the subdural spaces around the brain, so that they are able to renew their fluids. There is a clear separation of the auditory nerve into two branches (Fig. 230 *B*): the vestibular branch, with two rami innervating the semicircular canals, utriculus, and sacculus; and the cochlear branch, innervating the cochlea and the basilar membrane. The lagena (Fig. 230 *A*), which is the membranous duct coiled inside the bony cochlea, attaches itself at each side to the cochlear wall so as to form two other ducts, the scala vestibuli and the
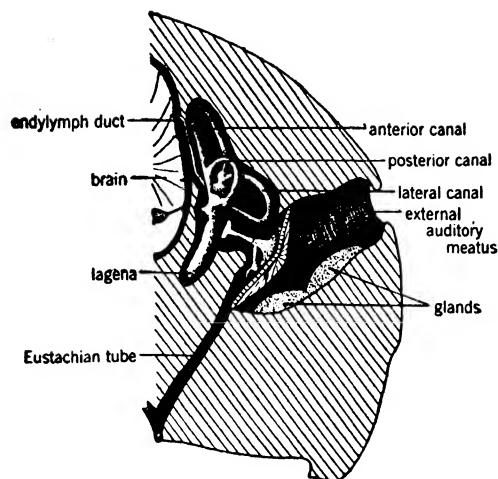
FIG. 224.   Ear of bird (Gallus) as seen from the posterior.
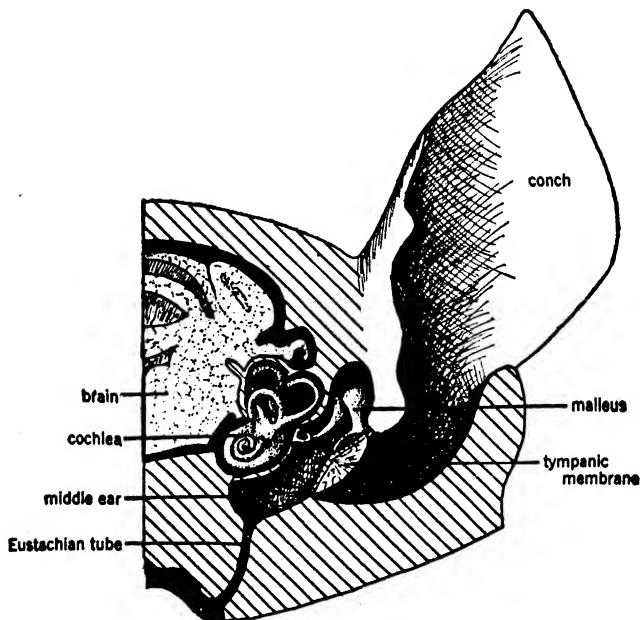
FIG. 225.   Ear of mammal (rat) as seen from the anterior.

scala tympani (Fig. 227 *A, B*).   The lagena itself, now called the scala
media, has a highly specialized structure, the organ of Corti, which is the
essential organ of hearing.   Its floor is the basilar membrane, its roof
Reissner's membrane.   The tectorial membrane transmits vibrations
to the hair cells.   The cochlear nerve extends along the modiolus, or
core of the cochlea, and its branches enter the basal membrane and
innervate the receptors, or hair cells.   A tunnel extends the length of
the organ, supported laterally by the outer and inner pillar cells.   Deiter's
cells (Fig. 229) extend from the membrane to the hair cells and act as
supports.   Henson's cells (Fig. 229) also serve as supports and are
probably not to be considered as sense cells.   Two windows open into
the inner ear from the middle, the foramen vestibuli (foramen ovale)
and the foramen tympani (foramen rotundum) (Fig. 230 *A*).   The
stapes fits snugly into the foramen vestibuli, acting as a plunger to
transmit the sound waves to the perilymph.   The foramen tympani
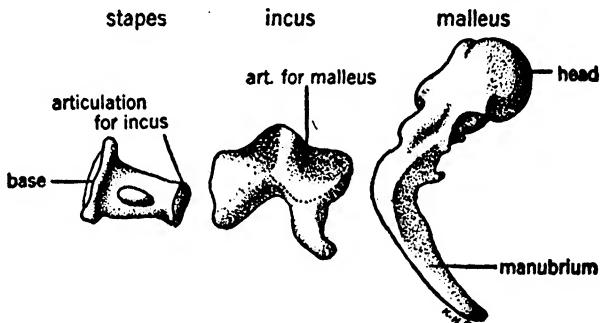
FIG. 226.   Ossicles of mammalian ear.

or round foramen, is a release valve, covered with a membrane.   It re-
lieves the pressure of the inner ear when the stapes is in action.   Several
theories have been advanced to explain the action of the organ of Corti
(Fig. 229), and how sounds are received in the structure of the cochlea.
One view has been that sounds enter any part of the cochlea and that a
re-distribution of the impulses is made in the brain.   A second view, and
one that appears to have the support of scientific investigation, is that
the parts of the organ of Corti are localized and that tones are received
in their appropriate focus of response.   Experiments show that the high
tones are received at the base of the cochlea and the low tones at the
apex.   Experiments on the easily exposed cochlea of the guinea pig
consisting of boring holes at definite parts of the spiral of the cochlea,
and then studying the results on hearing, seem to give favorable evidence
for the localization theory.   Animals in which parts of the organ of
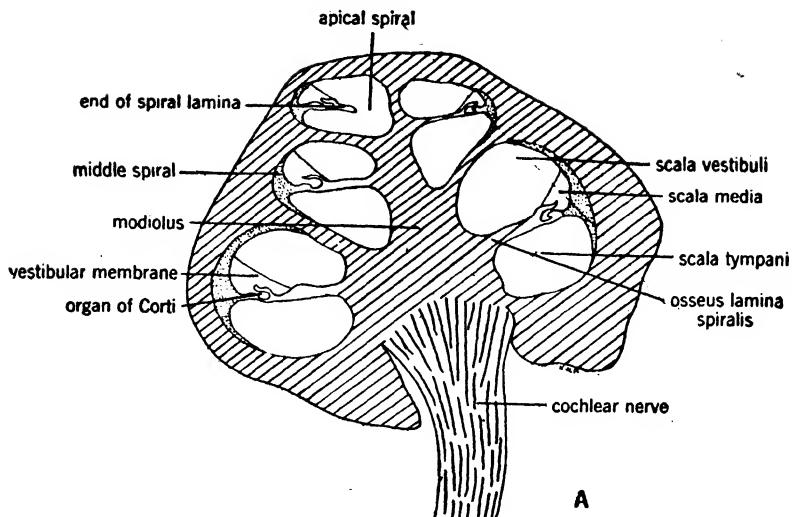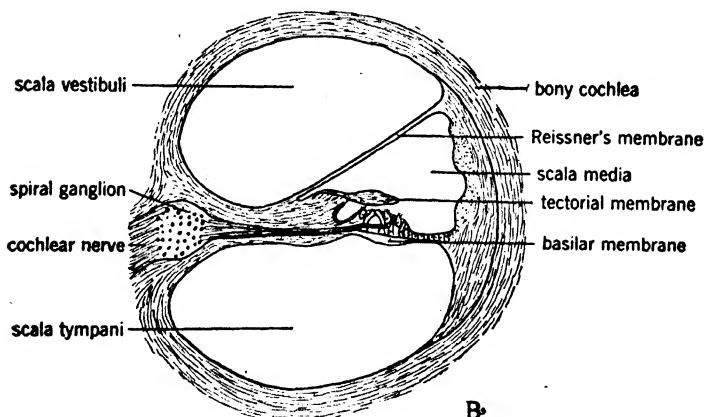
FIG. 227.   A, section of cochlea of new-born child (after Plate); B, section
through cochlea.   After Bütchli.
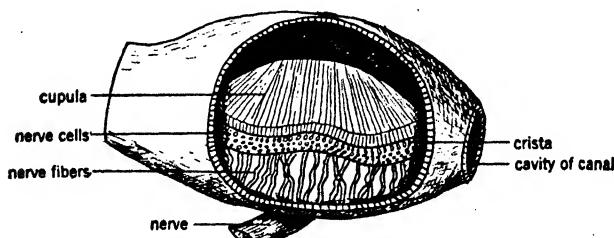
FIG. 228.   Ampulla of semicircular canal, dissected to show structure.
After Retzius.

inner hair cells
tectorial membrane
outer hair cells
Hensen's cells
limbus spiralis
Deiters' cells
basal membrane
outer pillar cells
tunnel
inner pillar cells
cochlear nerve
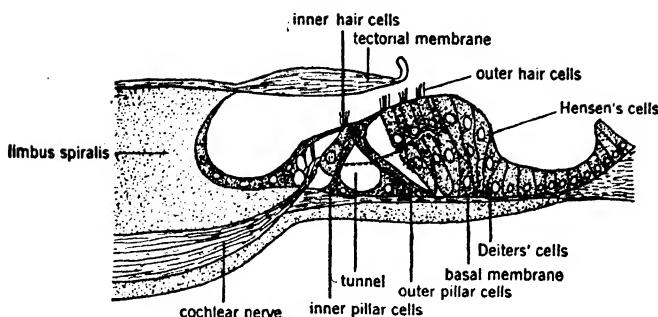
FIG. 229. Organ of Corti. After Retzius.

ant. canal
hor. canal
incus
stapes
endolymphatic sac
post. canal
VIII
VII
mastoid cells
malleus
sacculus
fenestra vestibuli
external meatus
cochlea
fenestra tympanum
tympanum
tensor tympani
perilymph duct
middle ear
tuba auditiva
A

macula utriculus
utriculus
post. canal
endolymphatic sac
ampulla of hor. canal
ant. canal
ampulla of post. canal
vestibular nerve
ampulla of ant. canal
median ramus of VIII
macula acustica
cochlear branch
cochlear duct
B

FIG. 230. A, diagrammatic section of mammalian ear; B, the membranous inner ear. After Weber.

Corti have been destroyed, show a definite loss of certain regions of the hearing band. Experiments of the same type, but using electrical contacts so that no part of the ear was injured, gave the same results. By these methods it was possible to map the cochlea of the guinea pig and mark the limits of the tone scale reception, and approximate the spot at which the different tone bands were received.

Middle Ear. — The middle ear is a relatively small (Fig. 230 A, B), air-filled chamber that is connected with the throat through the tuba auditiva (Eustachian tube), and closed at the outer auditory meatus by the tympanum or ear drum. This chamber contains the three ossicles, the mechanical parts through which vibrations are transmitted to the inner ear from the tympanum. Sound conduction of a coarser sort is also possible through the bones of the skull. The stapes (Fig. 226), the innermost of the three ossicles, is so placed that it closes the foramen vestibuli (oval window) and is thus in communication with the fluids of the inner ear. The movement of the stapes is of the pumphandle type rather than like a plunger. The stapedial muscle, a small slip, is attached to the neck of the stapes thus stabilizing its movements. The free end of the stapes, articulates with the incus, and there is a small cup, on the end of the stapes for this joint (Figs. 226, 230 A).

Incus, the second of these ossicles, is somewhat anvil shaped, and has two limbs or processes, the ventral, articulating with the stapes. A slight protuberance articulates snugly with a reciprocal cup on the stapes. This articulation of the incus, is sometimes free, instead of joined and is called the lenticular bone when separate. There is a good lenticular in the rat. The ossicle is attached to the wall of the inner ear by a ligament. A depression on the body of the incus supplies the articulating facet for the head of the malleus (see Figs. 226, 230 A).

The malleus of outer member of the chain of ossicles, is the largest of the three, and makes contact with the tympanum or ear drum. It consists of a head, two arms and usually an anterior process. The head fits into a facet on the incus and the arms are attached to the tympanic membrane. The tensor tympani muscle (Fig. 230 A), which takes its origin in the wall of the tuba auditiva, extends to the lower limb or manubrium and serves as a regulator of the tenseness of the drum. The drum is tensed for faint or indistinct tones, and loosened for loud noises that might injure the drum.

Outer Ear in Mammals. — The outer ear, or pinna, is foreshadowed in the Crocodilia where a movable scaly flap may open or close over the external meatus. A similar apparatus found in some birds (owls) consists of a fold of skin acting in the same manner. The pinna of the mammals is a cartilaginous conch composed of material borrowed from

the pharyngeal cartilages of the lower forms. It is present in all mammals, but for obvious reasons it is greatly reduced in water and burrowing forms.

The Eye

The eyes of all vertebrates are homologous structures, differing only in minor details, since an eye is just as useful in water as on land and no great change is required in the development of one from the other. The eyes of land animals have focusing lenses and glands to keep the surface moist. Primitively, the sense organs affected by light rays were located in the skin and independent to some extent, but in the evolutionary process they were taken deeper into the body and buried in mesoderm, later to extend again to the surface, as shown by embryonic development. The vertebrate eye is indirect in the sense that the rhabdomes, or light-perceiving sense-cells, are directed posteriorly and are not struck directly by the light rays; this is in contrast to the direct eye of the invertebrates in which the receptors are pointed towards the source of light.

In some members of each of the three lower classes (fishes, amphibians, and reptiles) there occurs a direct eye, called the pineal eye, on top of the head. Since there are two of these structures in some vertebrates, it seems probable that originally the median eye was paired instead of single. This median eye is not known to be functional in any living form. Experiments with *Sphenodon*, in which it is very well developed, have failed to show any reaction to light, although it has a lens, a retina, and a nerve connection with the brain. Since it is mechanically so well equipped and has retained a foramen through the skull, it is difficult to believe that it has never been functional. In mammals and birds this vestigial eye becomes the pineal gland.

Embryologically the eyes of vertebrates are developed from the walls of the telencephalon, although the anlage can be shown in the medullary plate. This plate follows the walls of the brain in its infoldings and outfoldings, and finally its position is fixed as the retina, with its receptors pointing towards the brain. A fissure remains on the ventral side, so that the optic cup is not perfect, and through this notch extend the ganglia of the nerves from the optic tract and the blood vessels of the eyeball. The lens originates as a thickening of the ectoderm over the optic cup, which sinks in and is cut off, and its concentric structure results from the growth of the cells in regular layers around this center.

The parts immediately concerned in the transmission of light in all vertebrates are: (1) the cornea, which is the transparent front of the

eyeball; (2) the pupil, controlled by a diaphragm, the iris; (3) the lens, by which the light is focused on the sensitive membrane, the retina (Fig. 235). The whole eyeball is surrounded with cartilage, or connective tissue, which protects it against distortion by pressure, and which also conducts the nerves and blood vessels into the structure. The cornea is a cleared section of the sclera covering the eye. The iris is usually pigmented, and it has three layers of pigment cells in mammals. By expanding or contracting the pupil, it controls the amount of light entering the eye. Its sphincter and dilator muscles are innervated by the autonomic system. The lens is held in place by the choroid coat, which develops the ciliary process, the ciliary muscle (Fig. 236), and the suspensory ligament known as the zonula ciliaris. In the lower vertebrates the lens is spherical, and the accommodation (or focusing of the image on the retina) is through slight anterior-posterior movements of the lens. In the higher vertebrates the lens (Fig. 236) is biconvex, and the accommodation is by changes in the shape of the lens itself, through the action of the ciliary muscle and process. There are two chambers (Fig. 236) in front of the lens: the anterior chamber, which is between the iris and the cornea; and the posterior chamber, which is between the iris and the lens and is limited by the ciliary process. These two chambers communicate with each other through the pupil and are filled with the aqueous humor. The eyeball proper (posterior to the lens) is filled with the jelly-like vitreous humor. The fluids of the eye are supplied through the lymph system. The optic tract enters the eyeball on the mesial side of the posterior pole.

Retina. — The retina (Fig. 231), which is the sensitive lining of the eyeball, is derived from nervous tissue and consists of a layer of nerve fibers, several layers of nerve cells, and a layer of rods and cones, the specialized light-receptors, the ends of which are imbedded in a layer of pigment cells. The nerve fibers, coming in from the optic tract, are spread in a network over the surface of the retina and thus make up the first layer through which the light passes. The ends of these fibers penetrate the deeper layers of the retina, forming connections with the nerve cells and granular cells that compose these layers, and finally reach the sensitive rod-shaped and cone-shaped receptors (Fig. 231). Since the rays of light must go through all these layers to reach the receptors, the intervening structures must be perfectly transparent. The " blind spot " of the retina is the point of entrance of the optic tract, since this area lacks rods and cones. The macula lutea is a yellowish spot on the retina near the posterior pole of the eye. Within the macula is the fovea centralis (Fig. 235), which is a thin spot on the
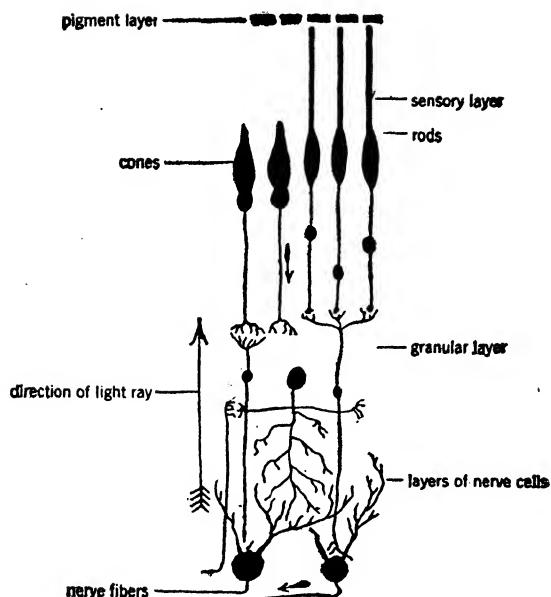
FIG. 231. Structure of retina. After Morris.
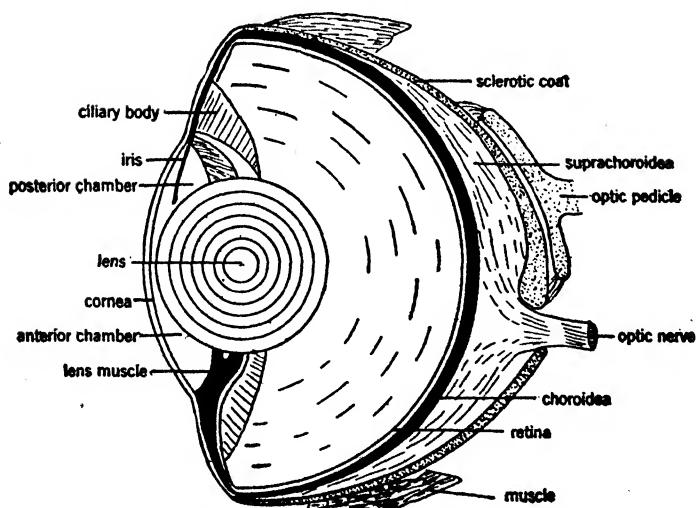
FIG. 232. Eye of shark (Squalus acanthias). After Franz.

retina where some of the layers are missing and where the rods and cones are especially numerous and vision is most acute. The retina extends anteriorly intact and ends in a wavy line, the ora serrata, where it ceases to be nervous. The tapetum lucidum, a thin shiny layer of pigment cells, is developed on the choroid coat next to the retina in
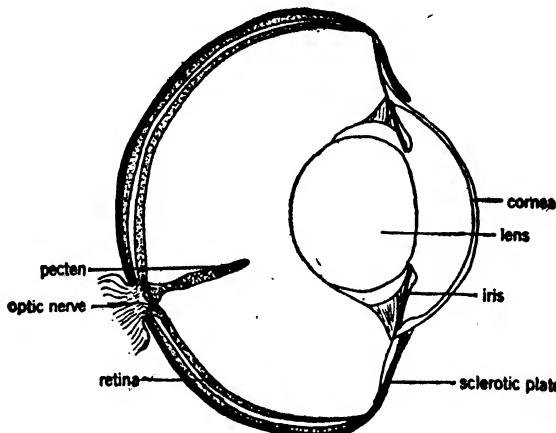
FIG. 233. Eye of lizard, diagrammatic. After Rochon-Davidneaud.
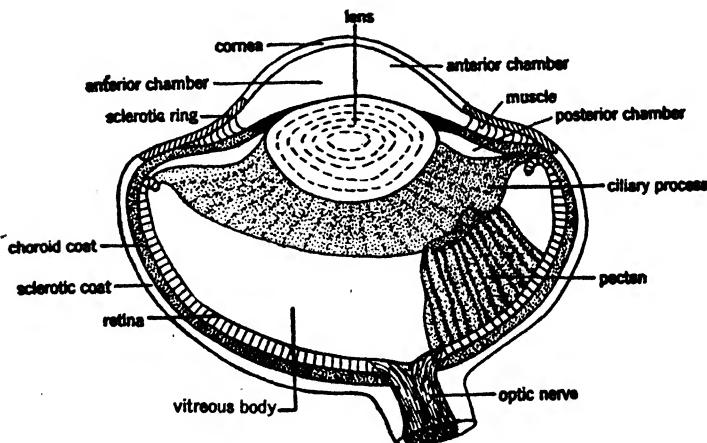
FIG. 234. Diagrammatic, sagittal section of eye of chicken.

some fishes and carnivores. This is very conspicuous in the domestic cat when exposed to a bright light at night. It is silvery in fishes, so that their eyes have a metallic color. It is supposed to aid vision in weak light. The visual purple is a pigment developed in the rods which fades on exposure to light. It is possible to get a photographic

image by exposing an eye that has been in the dark and fixing it im-
mediately in an alum solution.

The choroid coat (Fig. 235), which surrounds the retina and forms
the iris, is a highly vascular mesodermic layer, rich in blood vessels and
lymph spaces.
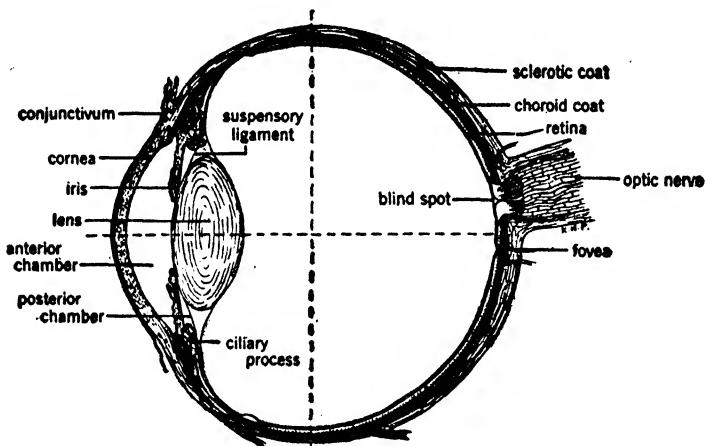
FIG. 235. Diagrammatic section of human eye. Redrawn from
Plate and Luciana.
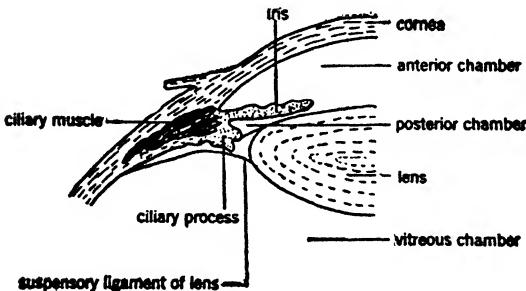
FIG. 236. Ciliary process and accessory structures of mammalian eye.
After Morris.

The sclerotic, or outer, coat (Fig. 235) is tough and fibrous and may be
partially of bone, since it is found ossified in all classes except the mam-
mals. Bony sclerotic rings appear to be a protection to the eye, in
preventing any change of shape under pressure, and they seem particu-
larly valuable to water animals and birds. The sclerotic coat corre-
sponds to the dura of the brain. The anterior region is cleared to form
the cornea. The optic tract and blood vessels must pierce this coat to
reach the interior of the eyeball.

The eye is so sensitive that it must be protected in every way to preserve its efficiency. The eyelids, found in most vertebrates, consist of a pair of movable flaps that close and permit the shutting out of light. Lids do not appear in the fishes but are found in all the other classes. In snakes the eyelids are grown together and cleared, so that the eye is open permanently. The conjunctiva is a delicate membrane that covers the eyeball and lines the eyelids. The lids with their glands prevent drying of moist parts and supply fluid lubricants. The eyebrows and eyelashes both contribute to protection from foreign matter. The nictitating membrane, a third eyelid, is prominent in lower animals, but in the mammals it is reduced to a small rudimentary structure in the inner angle of the eye, the plica semilunaris.

The glands of the eye, the Harderian on the inner angle and the lacrimal on the outer, come into prominence with land life. These glands are not present in fishes and are rather small in amphibians, but assume an important stage in reptiles, birds, and mammals. They are usually lacking or rudimentary in water-living forms of even the higher classes. Fluids from these glands are spread over the eyeball by the moving of the lids, the excess being carried to the nasal cavity through the lacrimal duct, which has two openings, the superior and the inferior, at the inner angle of the eye. The Meibomian or tarsal glands (modified sebaceous glands) spread a thin film of oil along the borders of the lids and prevent the overflow of the fluids. The ciliary glands open along the borders of the lids.

The falciform process found in some fishes extends from the retina to the lens and aids in accommodation. The pecten (Fig. 234), or comb, found in some reptiles and birds, is thought to be homologous to this process. The pecten is a peculiar, folded, fan-like body that extends out from the retina at the entrance of the optic tract, and in some cases comes in contact with the lens. It has been suggested that the pecten aids in stabilizing the internal pressure of the eyeball rather than in accommodation of the lens.

The modifications of the eye are due to the many different uses of the structure. Telescopic types develop in some deep-water fishes, where the vision must be difficult, and birds of prey have eyes modified to meet the need of a very keen sense of sight. *Anableps*, a peculiar fish that spends much of its time at the surface, has a double pupil arranged so that the animal can see in water and air at the same time, the retina being divided on the median line to correspond to the double pupils.

Sight is usually lost in forms living in darkness, but some vestiges of the eye remain, such as parts of the lens, nerves, or retina. The eye

of the mole, although buried under the skin, still remains as a fairly perfect eye. Blind forms occur in all classes except birds.

Résumé

Sense organs consist essentially of nerve endings, or receptors, which may be single (as tactile cells in the skin), grouped together (as in lateral-line organs and the ampullae of Lorenzini), or highly specialized, with complicated accessory structures (as in the ear, eye, etc.). Receptors are not limited to the surface of the body but are found also deep in the tissues and organs, making possible a great range of internal sensations, which are the physical basis of emotions. The lateral line, found in fishes and amphibians, detects low vibrations of the water. Taste, a limited sense, may have its end organs on any part of the body in fishes and amphibians, but in higher vertebrates the receptors of taste exist only in the mouth. The sense of smell in fishes is localized in a comparatively simple nasal capsule. In amphibians and amniotes the nasal capsules are connected with the mouth or pharynx. Jacobson's organ, accessory to the sense of smell, is present in most lower forms. The ear, found in all vertebrates, is probably a derivative of the lateral line. Originally the ear was an organ of equilibrium, with receptors limited to the semicircular canals, and later it developed an auditory function. The nerve center of equilibrium is in the cerebellum, while that of hearing is in the medulla. Tetrapods develop a middle ear (derived from a spiracle), with a stapedial plate (derived from the hyomandibular bone of the fish) and a rod or columella (derived from the symplectic bone). In mammals two additional ossicles are added, the incus (derived from the quadrate) and the malleus (from the articulare). The cochlea develops a complicated structure, the organ of Corti, sensitive to pitch and quality of sound. The innervation of the ear is through the auditory nerve with its two branches, the vestibular and the cochlear. The functional eyes of vertebrates are of a single type, in which the light-perceiving receptors are directed towards the back of the eye and away from the light. The eye is formed from several sources: the lens from ectoderm, and the retina from an outpouching of the brain, while mesodermic tissues form the outside of the ball and give it support. A small, direct, pineal, or parietal, eye may be present in fishes, amphibians, and reptiles; but this median eye has not been shown to have any function as a light-perceiving structure, though it has all the necessary parts, including a lens, retina, and nerve connections. The cornea, a cleared portion of the sclerotic coat, covers the anterior part of the eyeball. The iris regulates the amount of entering light, the lens focuses the rays, and the retina contains the receptors (rods and cones), which are imbedded in the pigment of the choroid coat. The retina itself is transparent and is made up of numerous layers. The blind spot on the retina is the exit of the fibers to the optic nerve, and the fovea is a small region where the rods and cones are most numerous and where sight is the keenest. The greatest advances in the eyes of higher vertebrates are in the better means of

keeping the eye moist, new protective structures, and devices that change the shape of the lens for better focusing. In mammals the visual center of the brain shifts from the mesencephalon to the cerebral lobes, although retaining a connection with the corpora quadrigemina. A tapetum, or shiny layer, may be present on the choroid coat. Peculiar processes, the pecten and falciform process, may be present, extending from the retina to the lens. Sclerotic bones, or eye-rings, may be present in all vertebrates except mammals.

UROGENITAL SYSTEM

The urogenital system consists of two kinds of organs, some reproductive and others excretory. The linking of the two functions into one system results in economy and convenience, inasmuch as the same ducts are used for both systems. It is assumed that originally each system had its own outlets to the exterior but that development and changes of structure in the vertebrate body made the combination desirable and thus reduced the number of openings into the body cavity. The sex organs are concerned in the production of ova and spermatozoa and in getting these products out of the body or in providing a place for fertilization. The excretory division of the system originated in the segmental pores and tubules of primitive chordates, in which there were direct outlets for wastes from the coelomic cavity to the exterior. In the Cephalochordata these tubules, or nephridial ducts, have ciliated openings, the nephrostomes, into the coelomic cavity, and also are associated with knots of blood vessels, so that the excretory products are taken from both the coelomic cavity and the vascular system. The sex products of *Amphioxus* are discharged into the atrial cavity and escape through the atrial pore. In the vertebrates the products of the kidneys are taken out through paired ducts, one from each organ. These ducts also carry the male reproductive cells, except in some fishes and amphibians.

Kidneys

The kidneys of the vertebrates are of three types, which may have represented at one time a long continuous structure that extended the length of the body. The pronephros, or " head " kidney, is functional in cyclostomes and in the young of fishes and amphibians, but is only transitory in other groups. The mesonephros, or middle kidney, is functional in fishes and amphibians (Figs. 240, 241, 242, 292). The metanephros, or posterior kidney, is the organ of excretion in reptiles, birds, and mammals.

The pronephros is placed well forward in the body, near the head. It is of segmental structure and consists of but a few tubules (numbering from one to thirteen) and a glomus, or knot of blood vessels. The nephrostomes provide ciliated openings into the metacoel, and the

pronephric duct collects the waste and empties it into the cloaca. The unit of structure is quite primitive when compared with that of the metanephros, since the connection between the glomeruli and the tubules is rather simple and of poor mechanical structure. In some forms (pronephros of frog embryo) the pronephric nephrostomes are cut off from the coelom, forming a separate chamber that compares with Bowman's capsule. The blood supply comes from the aorta.

The mesonephros, also segmental in origin, is posterior to the pronephros. It consists of a large number of tubules with a connecting
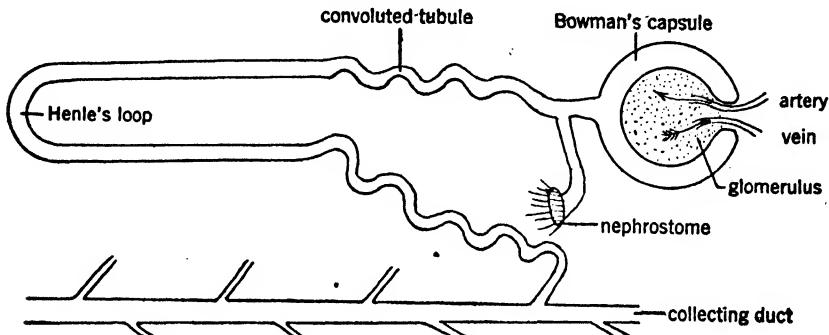
FIG. 237. Diagram of Renal unit. After Kingsley.
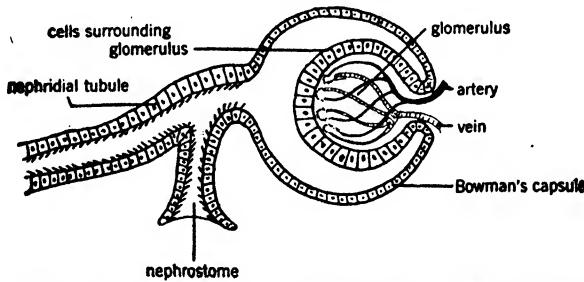
FIG. 238. Bowman's capsule, diagrammatic. After Kingsley.

mesonephric or Wolffian duct. This structure is the functional organ of excretion in adult fishes and amphibians. In the embryos of amniotes, it appears merely as a transient structure, soon to be replaced by the permanent kidney of the group. Functionally, it is a much better organ than the pronephros, for the tubules are much more numerous and the glomeruli are of better construction, since they are enclosed in Bowman's capsule, thus forming the Malpighian body (Figs. 237, 238, 239). The openings into the coelom, the nephrostomes, generally persist except in reptiles, birds and mammals. The mesonephros receives part of its blood supply from the veins of the caudal region and hind legs,

thus forming a renal portal system (Fig. 239). The veins break up into capillaries around the tubules and are gathered together by the venae revehentes and carried forward to the heart by the postcava. The blood supply to Bowman's capsule is through the glomerulus which takes its blood from the aorta.
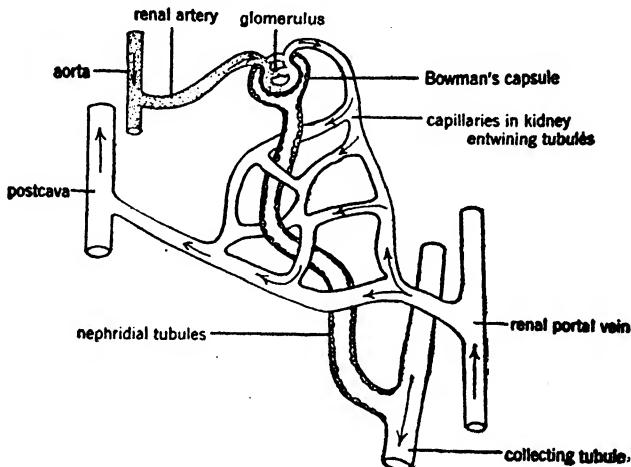
FIG. 239. Circulation around tubules of the kidney. After Curtis and Guthrie.
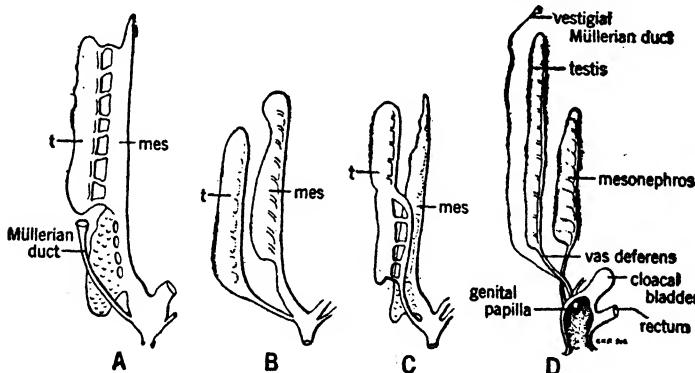
FIG. 240. Urogenital system of male fishes. A, Acipenser; B, teleost; C, Polypterus; D, Protopterus. After Goodrich.

The metanephros, or posterior kidney, is found in reptiles, birds, and mammals (Figs. 243, 244, 245). It does not show segmentation as clearly as do the more primitive kidneys. It originates from the base of the Wolffian duct near the cloaca and, extending anteriorly and dorsally, grows to the genital ridge of the coelom and receives a contribution from this ridge. The new duct, the ureter (Fig. 244), starting at the base of the cloaca, extends forward and expands and branches in

the body of the kidney to form a series of tubes which collect the excretion from the Malpighian corpuscles. The " pelvis " (Fig. 243) of the kidney is an enlargement of the ureter. This new tube, which drains the kidney, has no function connected with the reproductive system. The functional unit, or renal corpuscle, remains the same as in the mesonephros, but the nephrostomes are lost and there is no connection with the coelomic cavity. The blood supply from the aorta is greater, and the renal portal system, which was intimately connected with the mesonephros, no longer supplies blood to the kidney, although the veins still may pass through or over it. The kidney varies greatly in shape, being elongate in reptiles and bean-shaped in the mammals.
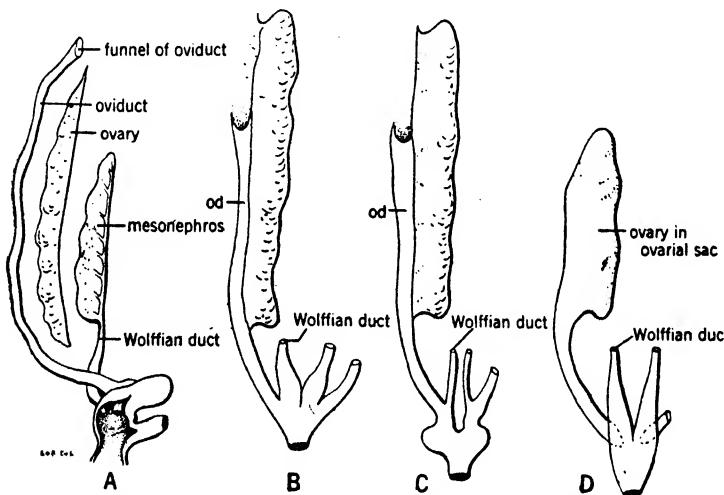
FIG. 241. Urogenital system of female fishes. A, Protopterus; B, Polypterus;
C, Lepidosiren; D, teleost. After Goodrich.

The lobular development, although retained in young animals, is generally lost in adults (Fig. 245).

The function of the kidney is to stabilize the blood stream, by extracting water and certain protein products of metabolism, together with other salts that are constantly being added from the tissues. The organic material extracted consists of urea and its compounds, uric acid, sodium chloride, phosphates, sulfates, and a number of other salts. In abnormal conditions, sugar and albumen may be drawn through the kidneys. The failure of the kidney brings rapid death from uremic poisoning. Selective action of the cells surrounding the glomeruli extracts water and waste products from the blood (Fig. 238). The cells lining the tubules are also selective, removing and saving certain products from the solution that passes them. In certain animals of

the desert, the water is reabsorbed by these cells, so that the urine is excreted as a solid.

COMPARISON OF THE THREE KIDNEYS

Pronephros	Mesonephros	Metanephros
Permanent in some cyclostomes, functional in embryos of fishes and amphibians, transitory in embryos of amniotes	Permanent in fishes and amphibians, transitory in embryos of amniotes	Permanent in amniotes
Few tubules (1–13)	Several hundred tubules	Several thousand tubules
Glomus imperfect with poor connection with tubules	Glomerulus surrounded by Bowman's capsule and well developed	Glomerulus well developed
Nephrostomes present	Nephrostomes present	Nephrostomes usually lost
Openings to coelom	Openings to coelom	No opening to coelom
Duct pronephric	Duct mesonephric or Wolffian	Ureter
Position anterior, near head	Position median	Position posterior
No urethra	No urethra	Urethra present
Pressure low	Pressure low	Pressure high
No renal portal present	Renal portal present	Going or gone

Bladder. — The urinary bladder is a variable structure, not found in all vertebrates. In some fishes a diverticulum from the cloaca is called a bladder, although it is independent of the ducts of the mesonephros. In some other vertebrates the bladder is formed by the fused ends of the Wolffian ducts. Amphibia have a small ventral diverticulum which extends from the cloaca and serves as a reservoir for urine. In snakes, crocodiles, and birds the bladder is missing, but in some reptiles and in all mammals it is formed from the base of the allantois. In mammals the connection is direct, as the ureters enter the posterior wall at its base. The urethra carries not only the urine from the bladder but also the seminal fluid of the male (Fig. 246 C).

Sex Organs

The sex organs of the vertebrates consist of the male and female gonads, that is, the ovaries and testes, with their accessory structures. There is a strict separation of the sexes except in the cyclostomes, which

are hermaphroditic (?).   Occasionally hermaphrodites appear in the higher
vertebrates, but they are anomalies and accidental.   The gonads are
compact organs that develop the ova and spermatozoa and bring them
to maturity.   Both ovaries and testes are derived from the epithelium
of the genital ridge of the dorsal region of the coelom, which is in agree-
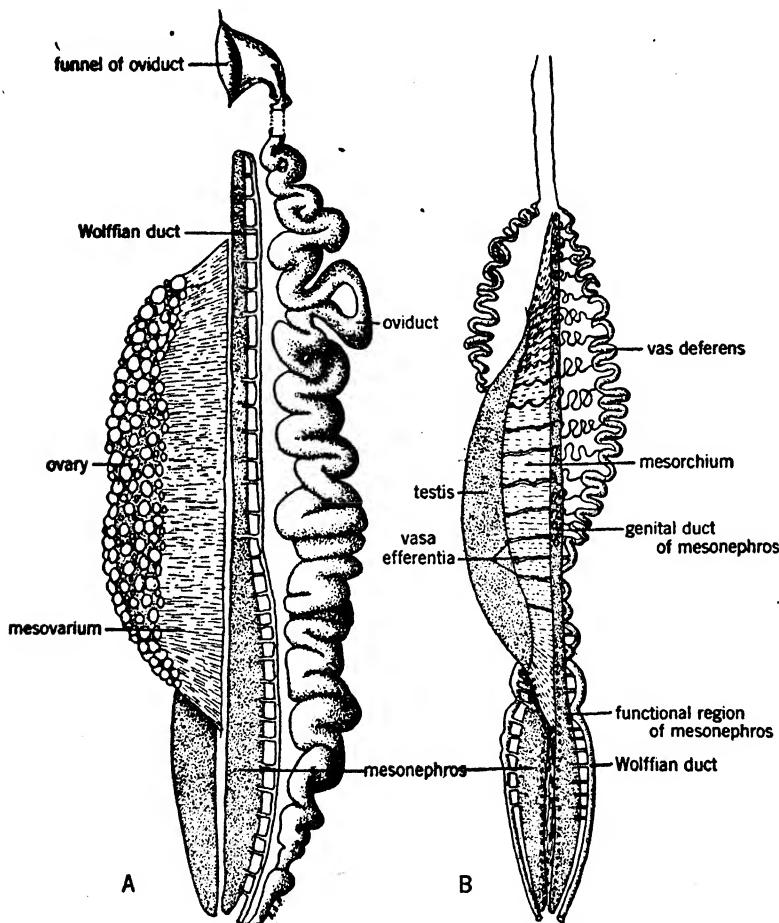
Fig. 242.   Urogenital systems of urodeles.   A, female; B, male.   After Chase.

ment with the hypothesis that the coelom is an expanded gonad cavity.
The gonads are normally located just anterior to the kidneys, except in
male mammals where the testes may change their position and come to
lie in a scrotal sac, which is a continuation of the coelomic cavity.   In
some mammals, however, they remain permanently in the body cavity,
and in some others they descend only periodically.   Experiments have

shown that testes placed in the body after being in the scrotum do not develop spermatozoa, perhaps because the body temperature is too high.

The fertilization of eggs varies, being internal in land animals and generally external in water forms. Some fishes are fertilized internally, and some amphibians form a spermatophore containing a large number of spermatozoa which is taken into the cloaca of the female for internal fertilization. Fertilization generally takes place near the anterior end of the Müllerian ducts. In all classes of vertebrates each individual goes through an embryonic developmental stage in which practically all the anatomical parts of both sexes are present, but while those of one sex complete their development, those of the other sex become partially obliterated and remain only as vestiges.

Female Reproductive Organs. — The female sexual organs consist of the ovaries (generally paired but sometimes single as in birds) and their conducting tubes, the Müllerian ducts, or oviducts, with their modifications and accessory parts.

FIG. 243. Sagittal section of mammalian kidney. After Radasch.

The ovaries, or germ glands of the female, are paired bodies, located at about the mid-region of the dorsal wall of the coelom, and lateral to the vertebral column (Figs. 241, 242, 279). Topographically they are usually close to the kidneys. They originate from the mesoderm of the genital ridge and receive primordial germ cells from a different source. The ovary is rather simple in structure, consisting principally of cells that are to become eggs and other cells that serve for support and nutrition. The ova are not in tubules as are the spermatozoa, but each ovum is surrounded by a number of cells which form a structure called the Graafian follicle (Fig. 247) in mammals. The oöcyte, or developing egg, is completely surrounded by cells at first, but by reorganization a follicular cavity is formed, filled with a follicular liquor. A stalk, the discus proligerus, attaches the egg, with its thin surrounding layer of cells, to the walls of the follicular cavity. No outlet is provided for the escape of the ripe egg, and it must burst through the wall, the ruptured area forming the corpus luteum. A rich blood supply insures

nutriment for the developing egg.   After its escape from the ovary, it is caught or forced into the oviduct through the ostium tubae.   The funnels of the two oviducts may be separate, or they may join to form a single opening as in the shark.   The ducts are modified according to the type of egg developed.   The large eggs of birds and reptiles must have specialized parts of the tube to supply the additional materials, so the duct is modified to supply food material, albumen, a shell membrane, and finally a shell (if one is present). The specialization of the mammal is very evident at the lower end of the oviduct.   The most simple condition, as in *Ornithorhynchus*, has the two oviducts opening separately into the urogenital sinus.   In the Marsupialia there is some fusion of the bases of the ducts to form a

FIG. 244. Diagram of mammalian kidney with its connections.

vagina, which may be double or even triple, according to the manner of joining of the tubes.   All placentals have a single vagina, but the uterus may be more or less divided, being two-horned, or duplex, in rabbits, bipartite in swine, bicornis in horses, and simplex in the primates and man (Fig. 248).

In placental mammals the egg is fertilized in the upper end of the Fallopian tube, after it enters through the ostium tubae.   It journeys down the tube and attaches itself to the wall of the uterus, where it establishes a connection through the development of a placenta.

FIG. 245. Lobate kidney of calf.

The ovary is held in place by ligaments that attach it to the posterior wall of the coelom.   The old ligament originally tying the mesonephros to the body wall becomes the *broad ligament*, which,

with the mesoarium, holds the ovary in place. The posterior part of this old ligament forms the *round ligament*, which ties the ovary to the pelvic cavity posteriorly.

Male Reproductive Organs. — The reproductive organs of the male consist of the gonads, or testes (Fig. 249), and their accessory structures.
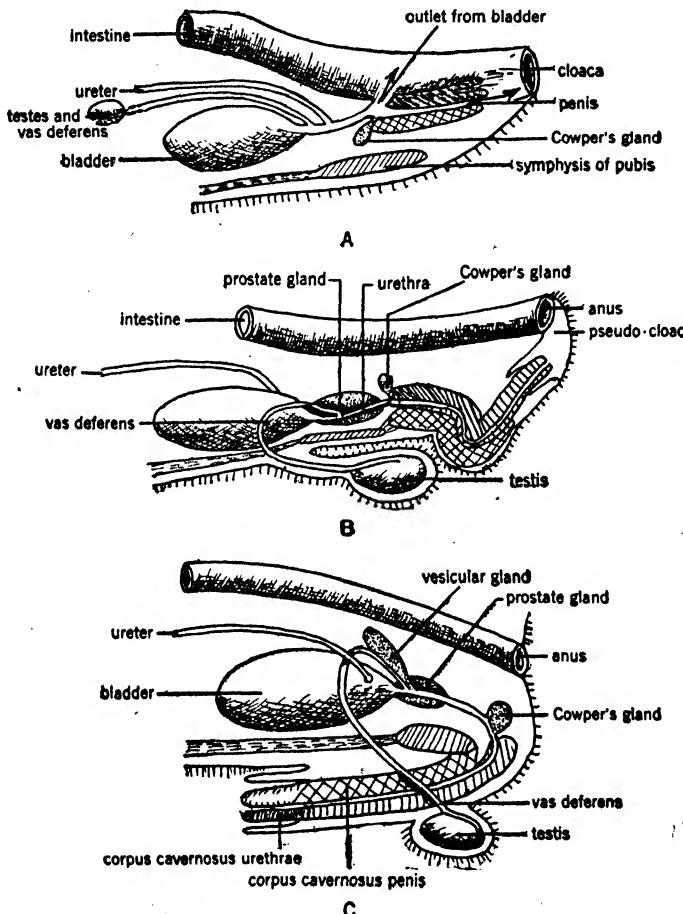
FIG. 246. Diagram of male urogenital systems in the three subclasses of the mammalia. A, monotreme (Prototheria); B, marsupial (Metatheria); C, placental (Eutheria). After Weber.

The testes generally occupy the same relative position as the ovaries, but in some mammals they migrate seasonally or permanently to the scrotal sac, which is a diverticulum of the coelom. The testes, unlike the ovaries, are made up of a large number of seminiferous tubules (Fig. 249) formed at the time of the migration of the primordial germ

cells. The spermatozoa develop in the walls of these tubules and pass through the *vasa efferentia* and other connecting ducts to be stored in seminal vesicles and later discharged in the process of the fertilization of the eggs. The ducts carrying the spermatozoa into the seminal vesicles are developed from the Wolffian ducts, which in the lower vertebrates continue to serve their original function as outlets from the kidneys. In the amniotes, with the development of the metanephros and its duct (the ureter), the Wolffian duct becomes the *vas deferens* and is used only for the products of the testes. The anterior part of the mesonephros degenerates as the ducts in this part become adapted for the conveyance of the spermatozoa. In *Acanthias* the anterior part of the Wolffian duct acquires a new outlet to the urogenital sinus (Fig. 278), and the posterior part retains its function as the outlet of the mesonephros. In higher vertebrates the *vasa efferentia* are greatly lengthened and much coiled, forming a structure called the epididymis. In amniotes the Wolffian or mesonephric duct is given over entirely to the sex materials, as the metanephros has its own outlet, the ureter.

With land life, internal fertilization was necessary and some kind of an intromittent organ had to be developed. Elasmobranchs may use the pelvic fins, as in *Acanthias*, but in the amniotes other structures are developed. The first type of the intromittent organ, found in snakes and lizards, is rather a makeshift structure, that of the snakes being a pair of sacs, the hemipenes, which can be everted in copulation. The spermatozoa are conducted along grooves, thus reaching the oviducts of the female. The second type, found in some reptiles, some birds, and all mammals (Fig. 246 *A, B, C*), is a single structure developed from the ventral wall of the embryonic cloaca. It consists of a ventral part, the corpus cavernosum, which encloses the urethra; two lateral parts, the corpora cavernosa penis; and a distal part, the glans penis. The material of these spongy structures is tough, fibrous, connective tissue, with large spaces in which blood collects, so that the penis is erectile. In some mammals an os priapi, or penis bone, is developed.

The *vas deferens* connects with the urethra at its proximal end, so that the urethra serves to conduct both the seminal fluid and the urine. The reproductive system of the male has a number of accessory glands, all of which help in the elaboration of the spermatozoa or in supplying them with fluids to assist in their transportation and nutrition.

The rat (Fig. 323) has four or five pairs of glands along the route that the spermatic fluid must travel, the prostate, vesicular, ampullary, and Cowper's glands, and probably the seminal vesicles — all of which assist in the formation of the spermatic fluid.

Since there is a stage in the development of the individual when all the sex structures are in an intermediate condition, a comparison of their homologous parts is rather interesting. Practically all the parts of one sex are present in the opposite sex as vestiges. The following table shows some of the homologies in mammals.
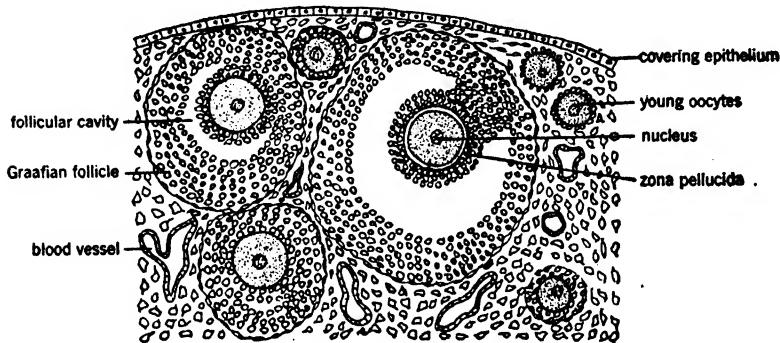
FIG. 247. Section of ovary of cat. After Jenkinson.

Male	Female
Testes	Ovary
Hydatid (Upper part of Müllerian duct)	Müllerian duct
Uterus masculinus	Müllerian duct
Epididymis	Epoöphoron
Paradidymis	Paroöphoron
Wolffian duct	Part of epoöphoron
Urethra	Urethra
Penis	Clitoris
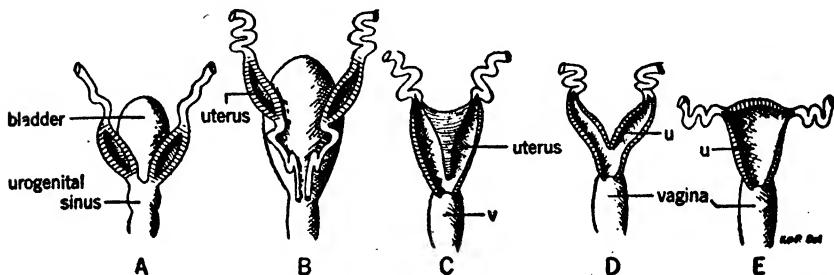
FIG. 248. Uteri of mammals. A, monotreme; B, marsupial; C, duplex uterus; D, bicornis uterus; E, simplex uterus.- After Weber.

Ovum and Spermatozoön. — The ovum, or egg (Fig. 247), is a specially developed body cell from a region set aside early in the development of the embryo. These cells migrate into position in the region that is going to be the ovary and form the basis for future egg development in the animal. The primordial egg undergoes a number of divisions until

finally some of these become the functional egg. The egg is distinguished by its size, since it generally carries food, and by its lack of ability to move. In the divisions of the egg the process of maturation cuts the chromosome number in half, and only one of the four cells formed by the maturation division becomes functional, the others being cast aside as polar bodies. The egg consists of the heredity-bearing bodies — the chromosomes — cytoplasm, food material, together with shell and membranes, where these are present. There is a direct relation between the food material and the way in which the egg develops. Since mammals of the placental type carry little food yolk, the eggs are very small (one-fifth of a millimeter in man).

The spermatozoa are developed in the testes, to which the primordial germ cells migrate in the development of the embryo. A spermatozoön
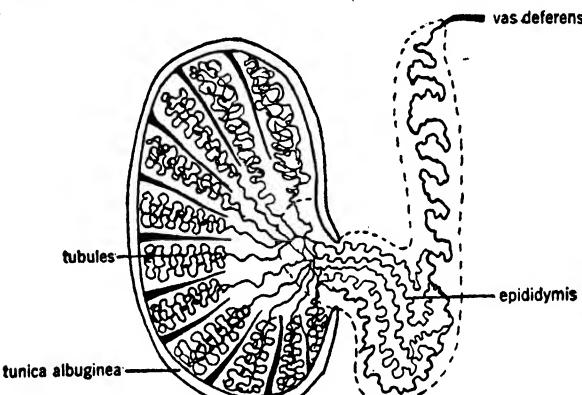
Fig. 249.   Diagram of structure of testis.   After Gegenbaur.

(Fig. 250) differs from an ovum in being much smaller and of a more complicated structure, in being motile, and in carrying no food material. In the maturation process all the resulting cells become functional. The typical spermatozoön consists of a head, which contains the hereditary material, a mid-piece, an accessory structure, and the motile tail. The special parts enable the spermatozoön to swim in water or to travel over the moist membranes of the female reproductive tubes until the egg is reached. Fertilization generally takes place in the upper end of the oviduct.

Throughout the vertebrates, development is by means of a fertilized egg, but the treatment of the egg varies greatly in the different classes. The more common condition consists of the development of an egg that is supplied with sufficient food to carry it through its developmental

stages, so that it is able to care for itself. This type of egg may be fertilized either before or after it is laid. In lower forms it receives no parental care and must depend upon the surrounding medium for proper hatching conditions. The term oviparous is applied to egg-laying animals.
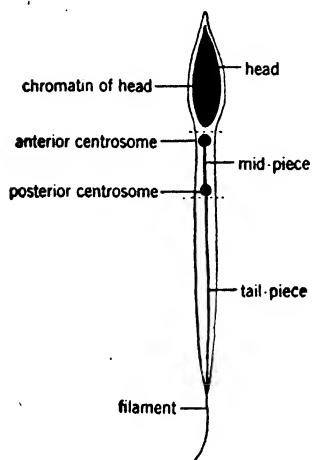
FIG. 250. Spermatozoön. After Jenkinson.

The opposite extreme is the viviparous type in which the egg is retained in the body of the parent until it has undergone part or all of its development. The viviparous condition varies from that in which the eggs are retained in the body, receiving no nourishment from the mother, to that in which all the food material is transferred to the embryo through a placenta. The term ovoviviparous is applied to animals in which the eggs are retained in the oviduct until hatched, but this condition intergrades with the strictly viviparous condition, so that its meaning is not clear. In all classes except birds, groups are found in which some provision is made for the transfer of additional food to the young, either through an omphaloplacenta or through an allantoic placenta, or both. Since the amnion and allantois are not present in fishes and amphibians, other means
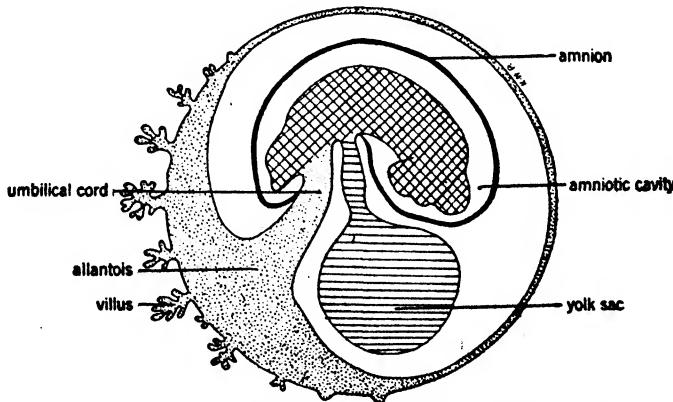
FIG. 251. Embryonic membranes of developing placental. After Weber.

must be developed for the transfer of food in the viviparous species, and generally this is the development of the omphalo-, or yolk-sac placenta.

The eggs of the fishes vary greatly in size, those of the Elasmo-branchii being the largest and those of the Teleostei the smallest. Fishes laying large eggs have a small number (10 to 20), but some of the teleosts (cod) lay more than a million. The young are provided with a supply of food which is contained in a yolk-sac, and this must be sufficient to carry them through their entire development. An early development of the heart and circulatory system supplies the embryo with means of distributing the food to different parts of the body and also provides the means for getting oxygen and removing waste. Whereas in most cases the egg is merely retained in the oviduct, in a few species an omphaloidean placenta is formed, which comes in contact with the uterine wall and is able to transmit food from the mother to the young and possibly to remove waste. *Mustelus laevis* and *Carcharias* of the Elasmobranchii have this yolk-sac placenta. *Pteroplatea microrura*, a ray, develops peculiar long villi in the walls of the uterus which enter the spiracle of the embryo and extend down into the esophagus, probably assisting in respiration and possibly in a transfer of food material. The bitterling, *Rhodeus amarus*, places its eggs in the gills of clams, where they burrow, living parasitically until they are ready to care for themselves. The sea-horses have a small marsupium which develops on the ventral side anterior to the pelvic fins, and in this the eggs are received and carried through development. Some of the catfishes carry the eggs in the mouth and gill chamber until they are hatched, and the young may return there for safety after hatching.

Practically all the amphibia are oviparous, and in addition most of them lay their eggs in water because of the metamorphic changes which make water necessary in the development of the young. The eggs carry some yolk but not a great amount and are surrounded by a jelly-like material which absorbs water when the eggs are laid. This is a sterile material which supplies some food and protects the young. There are some peculiar means of caring for the young. The European obstetric male toad fertilizes the eggs as they are laid and, wrapping them around his legs, keeps them there until they are hatched. The South American toad, *Pipa americana*, develops a series of pits in the skin of the back at breeding time, and in these pits the eggs sink and remain during all the developmental stages. *Rhinoderma darwini* carries the eggs in the vocal sac, retaining them until after metamorphosis. Some amphibians that live on rocks and trees lay their eggs in damp earth or leaves, covering them with a foamy material which preserves the mois-ture. These have a very short metamorphic period. *Ichthyophis glutinosa* coils around its eggs in its underground burrow. *Salamandra*

atra, a European form, is the only known amphibian in which ovoviviparity is approached. Its young seem to be reduced in number by cannibalism within the uterus, and only those that survive this uterine struggle are born. No shelled eggs occur in the Amphibia of the present day, and this is peculiar, since in every other class shelled eggs are laid by some of its members.

All the reptiles, birds, and mammals have two new membranes, the amnion and allantois (Figs. 251, 252). The amnion surrounds the embryo and forms a liquor-filled protecting chamber; the allantois spreads over the embryo and is an organ of respiration and excretion. Both these membranes are developed by the embryos themselves. Some reptiles are oviparous and others ovoviviparous, but egg-laying is the more common. The egg-laying forms may have a hard-shelled egg, as in the alligator, or it may be soft and leathery as in the snakes. The eggs are usually of comparatively large size and well supplied with food material. In *Phrynosoma*, the horned toad, both types of development are found in the same genus, since some lay eggs and others retain them and bear living young. Among the snakes, numerous groups are ovoviviparous, including the crotaline snakes, the gartersnakes, and some other water snakes. Two snakes have been found with an allantoplacenta, in which there is an evident transfer of materials from the mother to the young (*Denisonia suta* and *Denisonia superba*). It has long been known that the lizard, *Chalcides tridactylus*, developed both an omphalo- and an allanto-placenta, and (1929) Weekes found the same character in an Australian lizard of the genus *Lygosoma*. The strictly water reptiles, such as the sea-turtles and the fossil ichthyosaurs, had either to develop living young or come to land at egg-laying time. The turtle still comes to the sands of the shore to lay its eggs, but the fossil ichthyosaurs have been found with young in the body cavity, establishing the fact that they were ovoviviparous, with the possibility that some maternal connection was formed. The young were evidently born in the water, which is rather unusual for a reptile.

The eggs of birds are covered with a hard shell, and development is the same throughout the group. There is considerable difference, however, in the amount of food that is supplied, and for this reason eggs are large or small in proportion to the parental weight. The large eggs, with abundant food material, are able to carry the young to a stage where they are almost self-sustaining from the time of hatching; the smaller eggs have so little food material that the young are hatched in an immature condition, with no feathers and with closed eyes. The number of eggs varies from one to twenty or more, and with few exceptions they receive parental care. The cowbirds (*Molothrus*) deposit

their eggs in other birds' nests, and the Australian brush turkey makes a large mound of leaves, in which the eggs are deposited and left to shift for themselves. The penguin carries its single egg in an improvised marsupium between its legs.

The mammals differ from the other amniotes in that there is a reduction of the amount of food in the yolk-sac, since means of obtaining nourishment are provided by the placenta and later by the mammary glands. The monotremes lay eggs which resemble those of birds and reptiles and develop in much the same way, but the young when hatched obtain food from the mammary area of the mother. The marsupials retain the egg but there is little differentiation of the placenta, so that the young are born when very immature and complete their development in the marsupial pouch, supplied with food by the mammary glands. The allantois, in general, serves as an organ of respiration
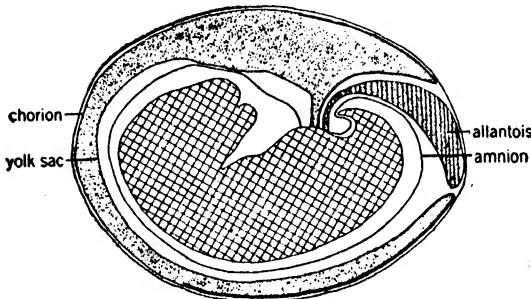
FIG. 252. Embryonic membranes of a developing marsupial. After Weber.

and excretion and in most marsupials never comes in contact with the wall of the uterus (Fig. 252), but in a few there is a temporary contact, and in *Perameles* a definite placenta is formed. The yolk-sac is quite large in the marsupials and surrounds the embryo, so that the allantois cannot reach through the chorion to the wall of the uterus. In placental mammals the placenta is perfected so that it transfers food materials from the mother to the embryo (Fig. 251). With the changed function of the allantois, the yolk-sac becomes reduced in size, since this provision of food is no longer necessary. The placenta is quite variable, both in actual shape and in its connection with the wall of the uterus. The allantois comes in contact with the chorion, which in turn makes a contact with the wall of the uterus through the development of villi (Fig. 251).

If there is no intimate growing together of the uterus and placenta, at birth the placenta pulls away free from the maternal tissues. The deciduate type forms an intimate connection with the wall of the uterus,

and at birth a part of the uterine wall separates off and is shed with the placenta. The shape of the placenta varies from the primitive type in which the chorion (Fig. 252) is completely covered with villi to that in which the villous areas are restricted to form cotyledons (in sheep), a band around the embryo (in most carnivores), or a disc-shaped placenta (in man).

EMBRYOLOGY

The study of the development of animals has greatly enriched the field of vertebrate zoölogy, since it has answered many questions in morphology that could have been answered in no other way. The impetus given to developmental studies by the evolution idea served to stimulate a large number of workers who were seeking to learn something of phylogeny and the mysteries of evolution through this tool. In one sense, the results have been disappointing, since many of the events occurring in the embryological development of the individual can hardly be considered a part of the actual history of the species. The telescoping and transposition of the changes, with a reversal of sequence in some cases, caused many misinterpretations of embryological stages. Many phenomena observed in the embryo represent nothing but developmental needs and have no evolutionary significance whatsoever. The embryo is developed under conditions that are hardly to be compared with adult surroundings, and, as would be expected, the embryo must solve its problems in its own way. Many conditions and structures met with in the embryo must be considered in their proper relations, and it is not always necessary that these structures have any relation to the past, present, or future development, but may be considered as purely embryonic adaptations. At one time, embryonic speculations were all interpreted as an indication of a part of the evolutionary history, but many of these assumptions have been discarded as untenable. There is, however, a certain similarity in development that extends throughout the vertebrates, and here, ontogeny and phylogeny have a proper place. Any organ or system may be studied in development and the exact sequence of its changes registered. In these studies, much valuable knowledge has been gained that may be used in determining the origin of some of the anatomical parts and their relation to the past ages. The embryological study of the chondrocranium, ear ossicles, excretory, circulatory, and nervous systems, and other structures, has added much that has been of value in clearing up origins. This study of the embryological history of parts has filled in many facts that would have remained unknown or problematical, if interpreted only from adult conditions.

All vertebrates start from a zygote formed by a spermatozoön and an egg, each a product of the gonads. The sex cells are of course directly continuous in their history with other cells of the body, but their differentiation appears to come early in the life of the animal. The eggs are always large in comparison to the spermatozoa, generally carry food material, and are non-motile. The spermatozoa are extremely small, carry no food material, and are motile. In internal fertilization the spermatozoa ascend the oviduct until the egg is reached. Eggs externally fertilized usually have the spermatozoa shed over them. There is probably a chemical action or attraction that accounts for the finding and penetration of the egg by the spermatozoa.
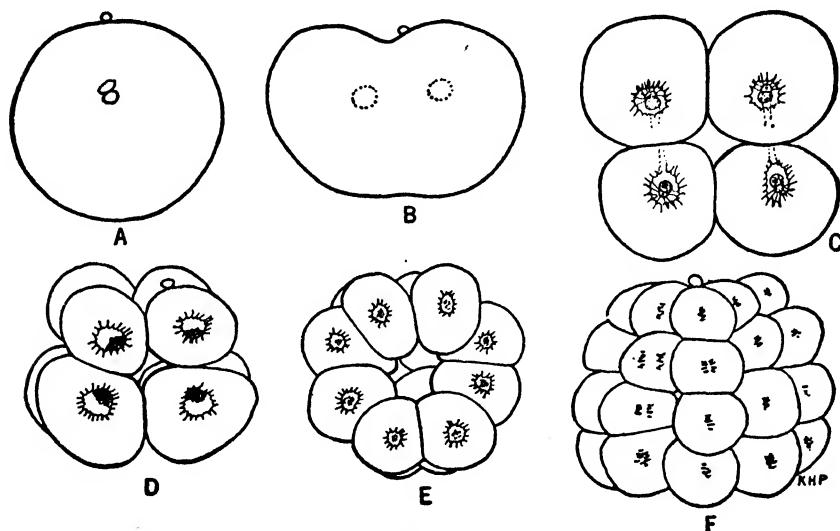
FIG. 253. Cleavage of the amphioxus egg. After Shumway. A, fertilized egg or zygote; B, dividing into two cells; C, four-celled stage; D, eight-celled stage; E, sixteen-celled stage; F, thirty-two celled stage.

When the egg and the spermatozoön fuse, they form the unit from which the new animal is to be developed, namely, the zygote, or fertilized egg. The zygote immediately begins to divide, thus forming a number of cells, or blastomeres. This division of the zygote into blastomeres is a perfectly regular process in eggs with little or no yolk, but becomes irregular when the egg is loaded with food, because the yolk-laden blastomeres cannot keep up with the rapidity of division of those which have little food (Fig. 253).

The first division is polar, dividing the zygote into two blastomeres; and the second is at right angles to the first, forming four. The third

division is equatorial, forming eight blastomeres, and is followed by two more divisions between the equator and the poles, thus forming sixteen cells. Rapid divisions follow until the cells finally arrange themselves so as to form a hollow ball with its segmentation cavity (Fig. 253).

In this blastula (Fig. 254), the lighter cells bearing no food are at the apical pole, and the heavier, food-laden cells are at the opposite pole, thus differentiating the two. By a process known as gastrulation, which varies in different forms, a two-layered structure, the gastrula, is obtained, the inner layer of which is made up of food-bearing cells and the outer layer of cells not containing food. Of the two layers so formed,
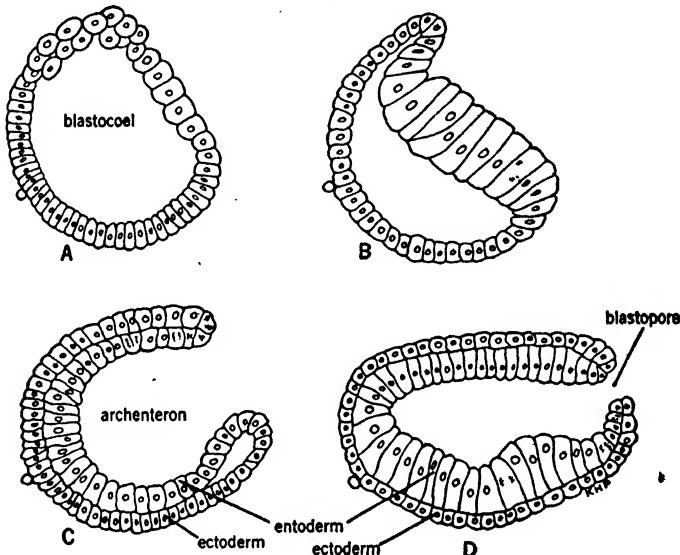
FIG. 254. Developing amphioxus. From Wieman, after Cerfontaine. A, blastula with flattened vegetative pole; B, invagination of the yolk laden cells; C, gastrula formed; D, completed gastrula.

the outer becomes the ectoderm and the inner the endoderm. The opening of the gastrula, or blastopore, is quite distinctive in the eggs of lower vertebrates. The gastrula (Figs. 254, 255, 256), develops rapidly and assumes polarity, so that there is an oral and aboral end. With continued development, a third layer, the mesoderm, is formed. This begins at the oral end with coelomic pouches that appear in the sides of the entoderm. These continue to grow and develop a cavity which is to be the coelom. A number of pouches develop in the head, only to disappear, but the others gradually enlarge and eventually cut loose from the parent tissue, thus forming the metameric, mesodermic somites. The pouches become differentiated into three regions, a dorsal epimere,

a median mesomere, and a ventral hypomere, each forming its part of the growing animal.

The epimere becomes differentiated into several regions: the dermatome, to form the corium of the skin; a sclerotome, to form the axial skeleton; and a myotome proper, to form the epaxial and hypaxial musculature. The mesoderm of the epimere grows ventrally, forming
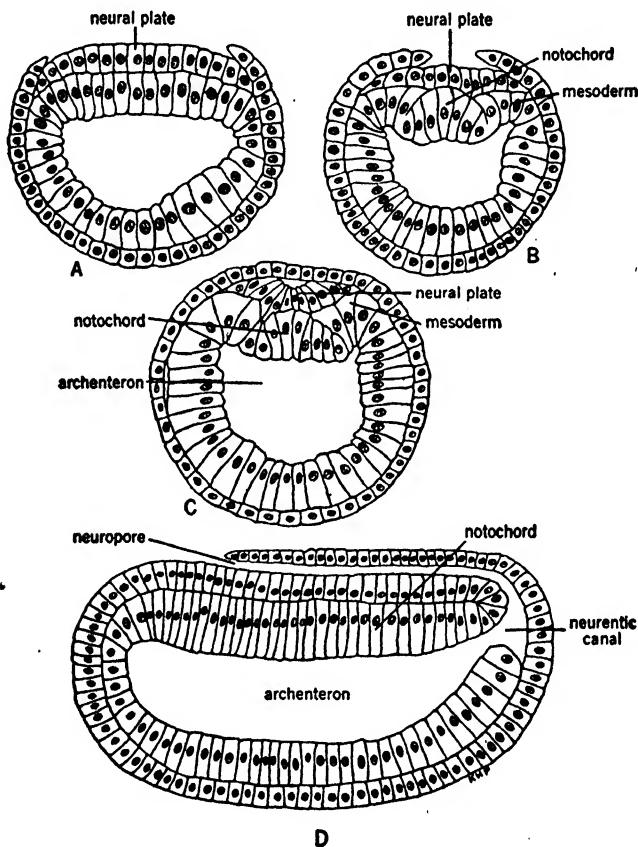
FIG. 255. Cross and longitudinal sections of developing amphioxus to show differentiation of layers and parts. From Wieman, after Cerfontaine.

the musculature of the body wall from its inner portion and the corium of the skin from its outer (Fig. 257).

From the mesomere are formed the organs of excretion and reproduction, together with their ducts, and parts of the circulatory system. The hypomere, which consists of two sac-like extensions along the side of the gut, eventually grows ventrally to fuse beneath the mesomere,

thus forming the coelomic cavity. The inner layer covering the gut forms the mesenteries and visceral peritoneum, while the outer layer becomes the inner lining of the body wall.

The mesenchyme, formed from cells of mesoderm and probably also from ectoderm and endoderm, is made up of scattered irregular cells, which pack in around structures, thus filling all spaces that are eventually to be connective tissue.
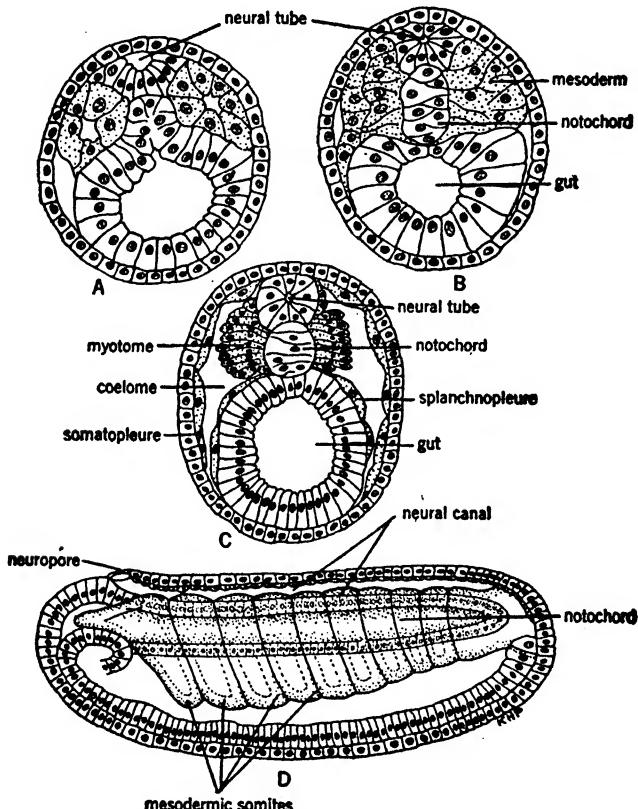
FIG. 256. Sections of developing amphioxus to show development of primary parts. A, B, C, cross sections; D, sagittal section. From Wieman, after Cerfontaine.

The endoderm continues to serve as the lining of the digestive tube, also lining all structures that are formed as diverticula, such as the liver, pancreas, and lungs. In an early stage a ridge appears on the dorsal side of the gastrocoele which is pinched off to become the notochord. Since this occurs at the same time that the mesodermal pouches are formed, there is some question as to whether the notochord is endodermal or mesodermal. In the higher vertebrates, the manner of
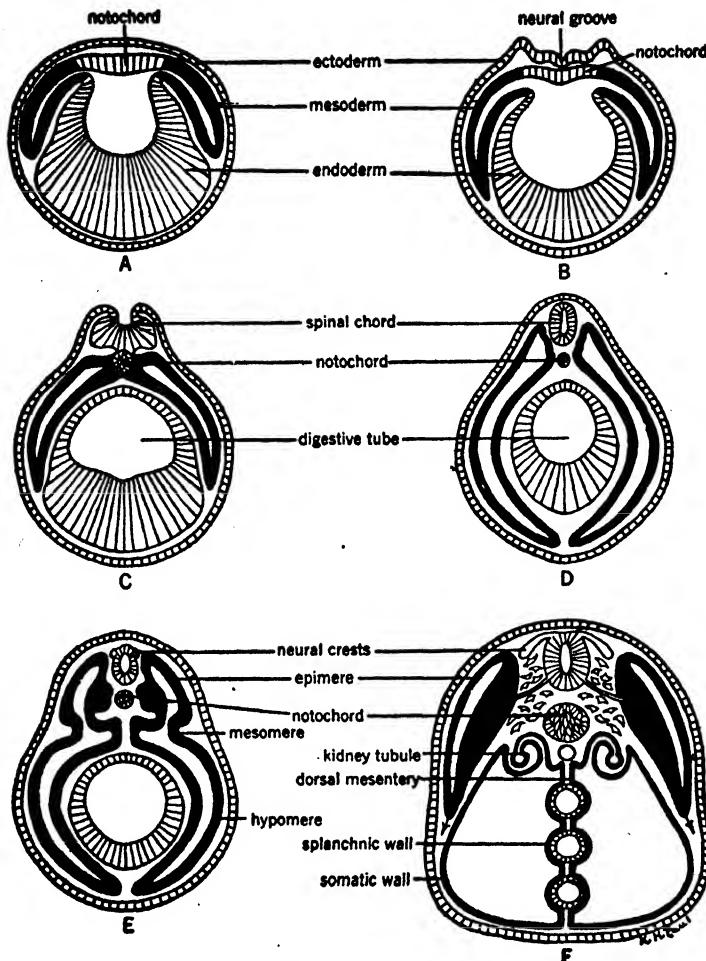
FIG. 257. Semi-diagrammatic cross section of anterior end of a developing verte-
brate (amphibian) to show the relations of the germ layers. A, early stage show-
ing the origin of the mesodermic pouches; B, early stage showing the neural
groove, neural ridge, notochord, and growing mesodermic pouches; C, stage in
which the neural infolding is almost complete, and the mesodermic pouches are
separated from the other tissues, and somewhat extended ventrally; D, neural
tube separate from the ectoderm, mesodermic pouches further extended; E,
advanced stage in which the neural crests are beginning to show, the mesoderm is
dividing into three regions, the epimere, mesomere and hypomere. Mesoderm
greatly extended to surround the whole body; F, epimere is cut away from the
rest of the mesoderm and starts a ventral extension that stops at the linea alba.
The mesomere is developing to form the kidneys and gonads, while the hypomere
is surrounding the digestive tube, forming the splanchnic sections which form
the mesenteries and the serosa of the digestive tube; and the somatic layer which
lines the coelomic cavity. The mesenchyme cells surrounding the neural tube
and the notochord are forming the vertebrae.

(294)

its origin suggests that it is mesoderm. The ectoderm and mesoderm are called upon to form a great variety of structures.

Derivatives of the different layers are summarized below:

(1) Ectodermal derivatives:
Outer layer of the skin.
Linings of the mouth, anus, and nasal passage.
Epidermal coverings such as horny scales, hair, feathers, horns, nails, spurs, enamel of teeth and of bony scales.
The nervous system entire, including the eye, nose, ear.

(2) Mesodermal derivatives:
Skeletal parts and muscles. Bony scales, and dentine.
Organs of excretion and reproduction.
Supporting materials such as cartilage, connective tissue, ligaments, tendons, and notochord of some vertebrates.
Circulatory system, including heart and vessels (lining in doubt).
Lining of the coelomic cavity.

(3) Endodermal derivatives:
Primarily the lining of the digestive tube and its derivatives, including the thymus and thyroid, lung, liver, and pancreas.
The notochord in some chordates.

The specificity of the germ layers suggested above is not absolutely rigid, since most organs are composite in their origin, being derived from two or three germ layers. Thus the stomach, lungs, tongue, and many other organs are composed of tissues from more than one of the primitive germ layers.

The eggs of the fishes and amphibians, developed in water, have a yolk-sac, but this is the single feature of these lower vertebrates that approaches the foetal membranes present in eggs that are laid on land, or in eggs that are carried by the mother until born or hatched. Land life had a very decided effect on the egg and its development, and reptiles, birds, and mammals have three new membranes, the chorion, allantois, and amnion, which are to become the distinctive features of these classes.

The food of the embryo, the yolk, is enclosed in the body wall, by the development of the embryo. In fishes, a definite yolk-sac is surrounded by the intestinal wall, so that it becomes an integral part of the embryo itself. This material is gradually used up, and finally the yolk-sac is absorbed. Many fishes, after hatching, have a large yolk-sac still present, which is used as a food supply until its possibilities are ex-

hausted. The large blood supply of the yolk-sac is for the transportation of materials to and from the embryo, and in mammals, where the yolk-sac is reduced, it is usually called the umbilical vessel.

Chorion

The chorion is formed by the upward growth of the body wall, which extends over the embryo in the head and tail region, and finally fuses. The inner layer of this fold forms the amnion and the outer layer the chorion (serosa or false amnion). In birds and reptiles the chorion forms a protective envelope, but in mammals, it develops into a much more important structure and is directly concerned in the attachment of the egg to the uterine wall (Fig. 252).

Amnion

The same fold that forms the chorion also forms the amnion, which is developed from the inner layer of this envelope, covers the embryo, and encloses it in a liquid-filled sac. This amniotic liquor is similar to sea-water in some respects, and replaces the ocean environment of eggs formerly laid in sea-water. The function of the amnion is protective, and the embryo in its liquid-filled cavity is insulated against minor shocks and disturbances that might injure the growing animal (Figs. 251, 252).

Allantois

A second outgrowth from the ventral part of the hindgut is a sac, which pushes out and enlarges until it may cover the whole embryo in reptiles and birds. In mammals, it becomes the attachment to the uterine wall, thus forming the structure that makes the connection between the growing animal and the mother. This outgrowth may be homologous with a diverticulum from the gut of the Amphibia, used as a bladder. The allantois of reptiles and birds serves as a collecting organ for wastes, as a distributing organ for food materials, and as a very important organ of respiration. Its surface is covered with blood vessels so that functionally it is very useful to the embryo. In some reptiles, the allantois may function as a connection between the embryo and mother, and the yolk-sac often serves in a similar way (Figs. 251, 252).

Placenta

Since viviparous forms appear in vertebrates, from fishes to mammals, it has been necessary for the embryos thus developed in the mother's body to have some means of disposing of wastes and of getting addi-

tional nourishment. The problem has been solved in a number of ways, and the yolk-sac, hair-like growths on gills, hair-like growths from the uterine wall, have been the means of supplying this nourishment. Viviparous reptiles may utilize the food supplied, but some other means of removing the waste and supplying food is desirable. The monotremes still retain reptilian and avian features in development, with the same use of membranes, since their eggs are enclosed in a shell and laid as in birds and reptiles. The marsupials are a stage in advance of the monotremes, but the young are born when very immature, and receive their nourishment through the mammary glands, to which they grow fast. Their foetal membranes are like those of the placentals, but the allantois, with few exceptions, does not make a contact with the uterine wall. The allantois of placental mammals always makes a contact with the uterine wall, and in these, the placenta reaches its highest development (Fig. 252).

Germinal Disc

The development of the germinal disc shows a series of events that have a similar aspect in all vertebrates. The disc develops on the top of the yolk-sac in eggs with a large yolk; in small eggs, with little or no yolk, the early development changes to fit conditions. From the dorsal surface the germinal disc shows ridges and a median groove that is the start of the nervous system. A rapid proliferation of cells changes the groove into a tube, completing the closure, and thus forming the embryonic brain and spinal cord. Beneath this activity of the surface, the other tissues are differentiating and the newly formed mesoderm is seen as tiny blocks along the side of the neural tube. Still deeper, the circulatory system is being laid down, and with a rapid growth of the blood vessels over the yolk, a food supply is readily available and the possibility of removing waste is set up.

It is possible to present but little in an introduction, since this is an extremely large field of zoölogy and should be studied in textbooks devoted to embryology.

Nervous System

The nervous system (Figs. 255, 256) is first considered because it is among the first to form and much of the early development is visible without sectioning. After gastrulation, there is a thickening along the future dorsal surface, and a medullary plate appears as a raised structure that is elongated and elevated above the rest of the surface of the ectoderm. In cross-section, this part becomes a deeper and deeper

groove, until it is finally roofed over, forming a hollow tube, enlarged at the anterior end for the future brain, the posterior part becoming the spinal cord.   The enclosed cavity becomes the lumen of the cord and the ventricles of the brain.   From the walls of this tube, the nerve cells and the nerves take origin.   The ectodermal nervous system is now sunken below the rest of the body.   Thus, what was the covering of the body becomes the lining of the nervous system.   The anterior part of the nerve tube now sends out outgrowths for the eyes and for the supra-segmental structures that appear on the dorsal side of the brain.   The
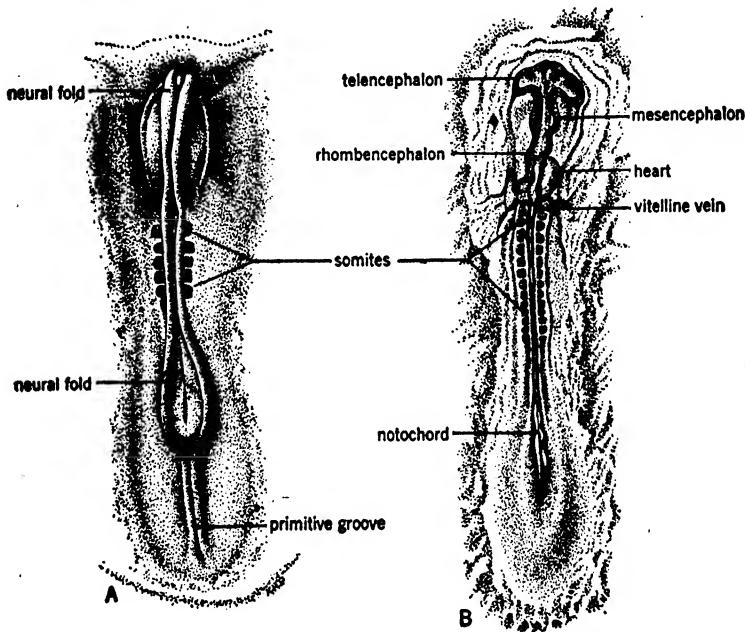
Fig. 258. A, 24 hour chick embryo. After Kerr. B, 33 hour chick embryo. After Shumway.

brain tissue differentiates into nerve cells of various types, and fibers for connections are formed and distributed.   The cranial nerves grow out to innervate their structures, and from the cord, neural crests appear that form the dorsal roots of the spinal nerves and the auto-nomic system.   The peripheral system is an outgrowth from the central structure, the fibers extending out and elongating until they reach the definitive tissue that they are to innervate.   From the motor region of the spinal cord, fibers are sent out that extend to the muscles, vis-cera, and other parts of the body (Figs. 258 *A*, *B*).

Development of Sense Organs

Eye. — The eye is a rather complicated structure, since several sources supply the material used in its formation. From the forebrain, an out-pouching shows at an early stage, which finally pushes out towards the skin, enlarges, and becomes a double-walled cup. A groove known as a choroid fissure extends along the under side of the stalk from the cup to the brain. The outer wall of the cup forms the pigmented layer, while the inner becomes the retina. From the ectodermal layer of the side of the head, which is in close proximity to the optic cup, an invagination occurs, forming an ectodermal body, the lens of the eye. The eye becomes surrounded with mesoderm, which supplies the material to form the outer covering of the eyeball, muscles, and other accessory parts. The sensory cells of the retina are connected, through the optic stalk, with the brain, thus forming the optic tract (Fig. 258).

Ear. — The ear is related to the lateral-line organs, and is formed by the invagination of the ectodermal auditory placode. The receiving cells are also ectodermal and derived from cells on the side of the head. The innervation and development both seem to point to a phylogenetic relationship with the lateral line. Starting as a pit, the vesicle differentiates into an utricular, vestibular, and saccular portion. The vestibular portion develops three ridges which pinch off and form the three semicircular canals. The attachment of the auditory pit to the ectoderm is marked by the endolymphatic duct in the shark. In higher fishes, the pit closes and the endolymphatic duct forms a connection with the meningeal spaces of the brain. The receptive cells of the ear are located in the ampullae of the three semicircular canals and in the sensory patches of the sacculus and lagena. In tetrapods, a middle ear is added to the hearing apparatus, derived from the spiracular opening, and other accessories are added, until the mammalian type is reached.

Nose. — The formation of the nose is similar at first to that of the ear, since a sensory pit sinks down deep to form the olfactory cup. Except in cyclostomes, the olfactory pits are paired, and in close connection with the mouth. The nose undergoes several major modifications in changing from a water- to an air-testing device.

Taste. — Taste buds, which are external receptors, are drawn into the mouth along with the ectoderm that lines this cavity, and may occur in the mouth or pharynx. They may also occur on the outside of the body, as in some fishes, where they may extend to the tail region (cat-fishes).

Skeleton

The skeleton is able to start its growth after the differentiation of the mesoderm, and, as this material insinuates itself between the other layers, the differentiation of the skeleton begins. The mesodermic cells are arranged in a layer around the body. The corium, immediately under the epidermis, is a source of skeleton building which makes up parts of scales, teeth, bony armor of primitive fishes, bony plates, the dermal plates of the skull, cleithrum, clavicle(?), episternum, gastralia, and other specialized parts.

Endoskeleton

In vertebrates, the nervous system is surrounded by a mesodermic layer, with horizontal and vertical septa, as well as material between the walls of the myotomes, and it is in this that the source of the skeletal material lies. The endoskeleton develops first by forming cartilage, which in turn changes to bone by a regular series of events through which the cells secreting the lime salts finally appear and dominate the growth.

Notochord

The notochord is a characteristic development of all chordates that is unquestionably the most primitive part of the skeleton. It has no predecessor in the invertebrates, and appears as a distinctive chordate feature. In *Amphioxus* (Fig. 256) it buds off from the dorsal side of the wall of the digestive tube, but in other forms it appears to take its origin from the primitive streak.

Muscular System

The muscular system forms simultaneously along with the skeletal system, and with few exceptions (ciliary muscle of the eye, and muscles of sudoriparous glands which are from ectoderm) it is from mesoderm. This includes the striated, smooth, and cardiac muscle. The mesoderm, arranged in sheets, along the sides of the embryo, becomes organized rapidly into mesodermic somites (Fig. 258), and these in turn become hollow and in cross-section show two walls, an outer and an inner. In a dorsal view of a developing embryo, these blocks show very distinctly at an early stage. The spaces between these blocks are invaded by mesenchyme cells so that a series of septa and cross septa are built up. The cells of the embryonic muscle masses elongate, develop contractile threads, and soon assume the appearance of muscle cells. The myotomes extend ventrally and dorsally to the midline, forming the much-modified musculature of the head, gills, and neck, as

well as the muscles of the body wall. The muscles of the limbs are formed by the downward extension of the myotomes into the limb buds, after the growth of the limbs. Besides the general body musculature, the involuntary system develops in the skin, around the viscera, blood vessels, and heart. These arise from the mesenchyme cells that have such an universal distribution throughout the body.

Digestive System

The digestive system (Figs. 255, 256) becomes tube-like and at either end has a short lining of ectoderm that has involuted at these two points, forming the stomodaeum or mouth cavity and the proctodaeum or anal cavity. The entire digestive tube, with these two exceptions, is lined with endoderm. There is an immense amount of activity in the digestive tract, and numerous outpouchings are produced to form the appendages of this system. The head region has teeth brought in by the infolding of the ectoderm where the scales become modified, changing their character and function. An evagination from the roof of the mouth, Rathke's pocket (Fig. 203), becomes associated with an outpouching from the brain, forming the anterior lobe of the pituitary body or hypophysis. The pharyngeal region is intensely active also with a series of pouches, some of which are represented by the gill pouches and their derivatives. A similar series of pouches appears in vertebrates above the fishes, but they become much modified and have various functions. A series of glands associated with these pouches play a prominent part in both and adult animals. In fishes, the pouches break through the body wall and develop gill arches; in most tetrapods above the amphibians the pouches do not break through, but leave a number of structures and glands as evidence of their former presence. The Eustachian tube of the tetrapod represents the remains of the first gill pouch, while the parathyroid, thyroid, thymus, and epithelian bodies are of great importance to all animals. The first outpouching posterior to the pharynx is the airsac of fishes, corresponding to the lung of the tetrapods. Posterior to the lungs, which starts as a median diverticulum, a single diverticulum forms the liver, and two or more form the pancreas. Other diverticula are present, such as the pyloric caeca of fishes and the caeca of reptiles, birds, and mammals; and there may be still other small outpouchings in the region of the rectum, such as the rectal glands of sharks or the bursa Fabricii of birds.

Circulatory Organs

Since metabolism must be carried on from the first cell divisions, the circulatory system is organized early in the development of the embryo,

so that the activities may be carried on under optimum conditions. The disc of the vertebrate embryo, resting on the yolk, must tap this food supply, and a series of blood vessels form outside the disc, on the surface of the yolk. These form a capillary net that connects with the embryo through the paired vitelline veins and starts embryonic circulation. These paired veins, joined proximally, extend forward beneath the gut, ultimately swing to the dorsal side of the gut, and become the dorsal aortae. Later they fuse at the posterior end, forming the aortic arches (Fig. 258). The heart, at first a straight tube, assumes an S shape in fishes, the sinus venosus and the atrium being dorsal to the ventricle. In the higher vertebrates, a four-chambered heart is attained by septa which divide first the atrium and then the ventricle, thus changing a straight tube into a four-chambered heart (Figs. 157, 258).

Veins. — The venous system develops at the same time as the arterial, to provide for the return of the blood, and this part of the system is much more complicated than the arterial. The primary parts are the two anterior and posterior cardinals. These must meet at the level of the heart where they form the ducts of Cuvier, which lead the blood into the sinus venosus and the atrium. This cardinal system is extended until it reaches all the organs. Veins conduct the blood from the posterior region of the body to the kidneys, where the vessels break up into capillaries and are conducted around the kidney tubules, while the intestinal blood is led to the liver, also breaking up into capillaries before being returned to the hepatic veins and the sinus venosus. The material forming the blood vessels, as well as the blood corpuscles, was termed angioblasts by His, and there is still some disagreement among embryologists as to the origin, but the greater majority consider the mesoderm as the germ layer that is the source of this material. In the forming blood vessels, cells called mesamoeboids appear, containing little haemoglobin, but as they develop into mature erythrocytes the haemoglobin appears.

Leucocytes may originate from this same mesamoeboid material. In mammals, the blood platelets are formed from parts of the protoplasmic processes of the giant cells developed in the spleen and bone marrow.

Urogenital System

The development of the urogenital system is usually taken back to the invertebrates, where the nephridia are paired in each segment, forming an opening from the body cavity to the outside of the body. In vertebrates, this is much modified, and there is usually a connection between the urinary system and the reproductive organs. Developing from the mesomere of the mesoderm, the pronephros is the most primi-

tive excretory organ, consisting of a small number of pairs (1–12) of ducts, a pronephric duct, and a very primitive glumerulus. The vertebrates have segmental tubules and but a single pair of openings to the outside, through the pronephric duct, which collects the products of the tubules. The mesonephros is a continuation of the material from which the pronephros develops, and the tubules grow out posteriorly to the primitive pronephros, but many more tubules are present in each somite, since they may number several hundred. These two structures are closely related in structure and in origin, but mechanically, the mesonephros is a decided improvement in a number of particulars. It also uses the pronephric duct as an outlet. The great improvement comes in the glomerulus with its capsule and its better blood supply. The metanephric kidney of reptiles, birds, and mammals, though closely related to the preceding structures, is quite different in that it is still more posterior in position, more compact, and has many more renal units. The nephrostome is closed, and a new duct, the ureter, now carries the waste to the bladder. The metanephros is formed from two sources, as is also the mesonephros. A diverticulum extends dorsally from the base of the mesonephric duct until it meets the mesodermal ridge, projecting from the dorsal wall of the body cavity. This diverticulum and this nephrogenic cord, form the kidney, with the ureter as the new duct. The new kidney has numerous renal units that unite and open into the pelvis or hollow of the kidney. The glomerulus, with its perfected Bowman's capsule and improved connections, is much better than the older renal structures. With the loss of the nephrostome, all connection with the coelomic cavity is lost. The long sinuous tubules have a rich vascular network, so that much activity takes place in this part of the renal unit.

Urinary Bladder. — The urinary bladder is a variable structure in the lower vertebrates that may be present or absent in the fishes. The fish type is formed by the fusion of the lower ends of the Wolffian ducts and a part of the cloaca, thus forming an urogenital sinus. The Dipnoi have a dorsal diverticulum from the cloaca that is entirely different. The allantoic bladder which arises from the ventral wall of the cloaca is fairly stable and present in most forms. The base of the allantois is thus connected with the urinary sac, while the rest grows out to perform its respiratory and excretory functions. At birth, the allantois is cut off at the body wall, and the solid ligament connecting the bladder and the body wall is the only trace remaining. The ureters retain their connection with the bladder as it grows, and the mesonephric ducts also retain a connection to the lower part of the bladder, which becomes the urethra or outlet.

Sex Organs. — The testes and ovaries develop from the genital ridge, along the dorsal region of the coelom. The origin for both sexes is similar, but as they develop, they diverge widely. Growing out from the genital ridge, each retains a connection with the mesentery, the mesorchium of the male and the mesovarium of the female.● The primordial male sex cells sink into the developing gonad, but form seminiferous tubules that always enclose the spermatozoa; the primitive ova, in contrast, are imbedded in the ovary and must break through the wall to escape. The ducts through which the products of the sex glands escape from the body are both related to the old Wolffian duct, from which the Müllerian duct of the female is split off, while the male amniote uses the original Wolffian duct. The adults of both sexes show numerous vestiges and remnants of the indifferent developmental stage, such as the traces of a vestigial Müllerian in the male. Tetrapods and internal fertilization changed the external genitalia materially. The genital opening in an early indifferent embryonic stage is quite similar in both sexes, that of the female remaining comparatively simple, while that of the male develops a phallus or intromittant organ from the same structure that remains as the clitoris of the female.

Résumé

The urogenital system comprises organs of reproduction and excretion. The chief organs of excretion, the kidneys, are probably related to the original metameric tubules of primitive forms. Kidneys are of three types: the pronephros, found in the lower chordates and in the embryos of others; the mesonephros, found in fishes and amphibians; and the metanephros, found in reptiles, birds, and mammals. The functional unit of the kidney is the Malpighian corpuscle, consisting of a glomerulus (Bowman's capsule), convoluted tubules, and collecting ducts. The mesonephros empties through the Wolffian duct, and the metanephros through the ureter. The urinary bladder is variable in origin and structure and is not always present. The female reproductive organs consist primarily of a pair of ovaries, and the oviducts may be divided into regions with special functions. The male reproductive organs consist primarily of a pair of testes, with ducts usually borrowed from the excretory system. Numerous accessory glands, associated with the discharge of spermatozoa and ova, are developed in the higher vertebrates. Ova are supplied with food material and are non-motile. Spermatozoa are motile and are relatively small and very numerous compared to ova. The eggs of fishes and amphibians generally are fertilized externally; those of amniotes are fertilized internally, usually at the upper end of the oviducts. The amnion and the allantois are embryonic membranes developed in higher vertebrates, and the allantois becomes the basis for the placenta in mammals. The fertilized egg, or zygote, by a division of its cells, forms a blastula, then a gastrula,

and finally an embryo in which three germ layers become differentiated — the ectoderm, the mesoderm, and the endoderm.

Three membranes, the chorion, amnion, and allantois, are characteristic in reptiles, birds, and mammals (Fig. 251). The chorion, formed from the body wall of the embryo, supplies a protective envelope in reptiles and birds and attaches the egg to the uterine wall in mammals. The amnion develops also from the same fold as the chorion, and surrounds the embryo with a liquid-filled sac. The allantois, an outgrowth from the hindgut, forms a large covering sac in reptiles and birds, supplying a large vascular surface for respiration and excretion; in mammals, the allantois changes its character, and is attached to the wall of the uterus, forming a medium of exchange between the mother and embryo. With the formation of the germ layers, the organs and systems begin to unfold. The digestive, nervous, circulatory, and excretory systems are laid down early in embryonic history. The ectodermal folds along the midline of the back sink below the surface, form a tube, and keep pace with the growth of the embryo in nerve supply. The eye develops as an outpocketing from the brain, to form a double-walled cup; the lens is formed by an inpocketing of the ectoderm over this cup. Mesoderm invades the eye and surrounds it, forming the sclera, muscles, and accessory parts. The ear is related to the lateral line and starts as an inpocketing from the auditory placode, carrying with it the sensory receiving organs. Taste buds are drawn into the mouth along with the ectodermal lining. The mesoderm differentiates early and starts the formation of the skeleton, the muscular system keeping pace with it. The digestive system, lined with endoderm, has outpocketings in the neck and body regions to form the numerous appendages of this system. Circulation starts with the first growth of the animal for the transportation of food and waste. The heart and blood vessels start early in the development of the embryo. The excretory system, starting with a simple pronephros, changes to a mesonephros in fishes and amphibians, and to a metanephros in reptiles, birds, and mammals. Testes and ovaries develop from the genital ridge. This system makes some striking changes in the shift from water to land.

CHAPTER XII

ENDOCRINE GLANDS

The endocrine structures consist of a number of glandular bodies that play a very important part in the lives of all vertebrates, from the first developmental stages to death. Though not clearly recognized as yet, it is probable that similar functions are performed by some substances in the invertebrates. It has been shown recently that plants have materials comparable to the hormones of animals. The hormones are chemical substances that are formed in the endocrine glands and distributed through the blood stream; for this reason the endocrine glands are called ductless glands. For the most part, the endocrine glands are small bodies, although some may have quite an appreciable mass of material; and although some of them have ducts, these ducts are not connected with the endocrine system. The action of these materials is quite rapid, and one of the features of a hormone is the extremely small quantity necessary to accomplish results. The endocrines exercise a control over the body somewhat comparable to the action of the nervous system, but in a different way, since the endocrine control is chemical. They appear to be responsible for correlating growth, both in initiating and in stopping it; for correlating the processes of metabolism; and for establishing a system to maintain the relations between the different body tissues. Although these glands appear to have certain definite functions, they also tend to check one another; if one gets too active, it in turn is checked by the action of another gland. They are specific not only for the animal from which they have been taken, but for other animals as well, since glandular extracts of one group seem to have similar effects on animals of an entirely different class. Knowledge of the action of the glands is obtained by several types of experiments, such as removal of the glands, introduction of the extracts, grafting of glands, and a wide range of these procedures.

Although most of the knowledge of the endocrines has been developed in the last three decades, it is certain that some of the structures, and even their actions, have been known for centuries. Since castration in both man and animals has been practiced for a long period of time, it is probable that the effects of this operation were among the first to be known and recognized. The old custom of eating adversaries to gain their strength and valor may have had its origin in the belief that there was a transfer of these qualities via the digestive tract. The idea of

eating parts of animals as cures for illness in corresponding organs has had a prominent place in medical lore, and even today has followers. Eating brains, livers, lungs, and gonads is an old practice. From the Greeks to comparatively modern times, there has been some knowledge of the glands and something of glandular action, but the real knowledge had to wait for the developments of the comparative anatomists, the experimental physiologists, and zoölogists, the microscope, and the findings of chemistry.

Leaving the rather hazy ideas of the ancients, the first real work on endocrines was done by Johannes Müller, who wrote on internal secretions as early as 1833. Bertold, in 1849, transplanted testes in capons and commented on the results. Brown-Sequard worked on organ therapy and performed some experiments on the secretions of the gonads. The name "hormone" was coined by Bayliss and Starling in 1906, when they made the discovery of secretin from the duodenum. They considered these materials as "chemical messengers." During the last thirty years the interest has increased, until now endocrinology has a very important place among the experimental sciences. The medical profession makes extensive use of the endocrine materials, and a number of them, such as thyroxin, pituitrin, epinephrin, cortin, testosterone, and estrone are available. Some of these have been prepared

FIG. 259. Diagram showing the location of the more important endocrine glands of man.

synthetically, but they are usually prepared from the glands of some animal that is readily available and can furnish a large supply.

The principal endocrine structures consist of two in the head region, the pineal and the pituitary; four in the neck, the thymus, thyroid, parathyroids and ultimobranchials; at least three in the body cavity, the pancreas, adrenals, and the gonads. It is possible that others will be discovered as the knowledge of their action and structure increases (Fig. 259).

Pineal

The pineal structure, or epiphysis, is a small outpouching from the roof of the diencephalon, the second division of the brain (Figs. 208, 209, 211). It is found in all animals and has a number of forms. In the lower classes of vertebrates, the pineal reaches the roof of the skull, and there is often a foramen associated with this gland, piercing the roof either through the frontal or parietal bones. In mammals it appears as a pinkish pouch that is covered by an overgrowth of the cerebral lobes and it is much more gland-like than in the lower animals. The nerve supply comes from the brain and the autonomic system. The status of this as an endocrine has been doubted, although when disturbed by tumors or other abnormalities, there may be an acceleration of growth, precocious development of the mentality, and premature sex development. Experimental evidence has been rather contradictory in character, but recently this evidence has become more positive. White rats, in which the pineal had been removed for a number of generations, showed definite effects that place the pineal in a different light. In these experimental animals, the number of litters was increased, but the size of the young and their subsequent growth were retarded. Later generations matured sexually in about half the number of days, but the size was considerably less than that of the normal animals. A definite retardation of growth appeared to be caused by the removal of the pineal in these experiments.

Pituitary

The pituitary gland is on the lower side of the diencephalon and appears to be a structure present in all vertebrates and probably in the protochordates. The pituitary is one of the oldest of the known endocrines, since its written history starts with Aristotle, Galen, and the early anatomists. Its embryology was first made known by Rathke (1838), who showed that it was formed by an outpouching from the brain that extended out from the floor of the diencephalon, and a corresponding outpouching from the roof of the mouth, the Rathke's pocket of anatomy. These two structures come together so that the Rathke's pocket extends anteriorly, forming the anterior lobe, while the infundibular pouch from the diencephalon extends posteriorly, forming the posterior lobe. Little of its function was known until early in the eighteenth century, when it was associated with certain abnormalities that occur in man, acromegaly, giantism, and dwarfism. Acromegaly is the result of a hyperactivity of the gland in the adult, causing certain parts of the skeleton to grow in a most startling manner

until finally normal proportions are lost. Giantism is also the result of hyperpituitaryism in the young animal, and though growth may extend far beyond normal, the animal remains proportional and normal in features other than size. Dwarfism results from the hyposecretion of the anterior lobe in the young animal, and here again the reduction in size is proportional, so that the end result is an individual much dwarfed but with all parts of the body in proportion, the midgets so familiar in the sideshow and circus.

Early in the study of the gland, it was recognized that the anterior gland was quite different from the posterior in action, and that the removal of the anterior gland usually caused death. Recently, however, it is understood that the probable cause of death is not the removal of the gland, but injury to the brain in the region of the tuber cinereum. The importance of the pituitary has increased with a more thorough

FIG. 260. Sagittal section of human hypophysis. After Morris.

understanding of its many functions, and it is now considered as a kind of master gland, since among its important functions is included control over some of the other endocrine structures and their secretions.

The pituitary is well established in the cyclostomes, but there is a peculiar relation to the hypophyseal sac, which opens into the narial passage, and also to the pharynx. From fishes to man, the pituitary is always a prominent structure on the ventral side of the diencephalon (Figs. 203, 205, 208, 260, 210). Anatomically, the pituitary consists of four parts, the anterior lobe, pars tuberalis, pars intermedia, and the posterior lobe. The infundibulum carries its lumen with it, extends posteriorly, and becomes glandular at the posterior end, thus forming the posterior lobe. Part of the infundibulum may become much folded, thus forming the saccus vasculosus of the shark and other fishes. The pocket of Rathke pushes dorsally and anteriorly, also carrying its lumen with it, and comes to lie between the infundibulum and the brain case. The intermediate lobe of the pars intermedia is between the anterior and posterior lobes, varying in size from a very distinct section to a very small region and sometimes appearing to be missing entirely. The pars tuberalis is a portion of the gland that develops at the base of the infundibulum, partly surrounding it, and in very close association with the brain. Both the intermediate lobe and the pars tuberalis are considered as parts of Rathke's pocket. The color of the pituitary

is quite different from that of the brain, and the gland is of sufficient size so that it is unmistakable even in small vertebrates. In many of the higher animals the pituitary is so surrounded by the sella turcica that it remains with the skull when the brain is lifted from the brain case. In lower animals the pituitary is easily reached through the roof of the mouth, but in the higher animals the easiest approach is through the nose and the roof of the nasal passage or through the side of the skull. Striking changes occur in the gonads, thyroids, parathyroids, thymus, and adrenals when the pituitary is removed. Since experimental removal may injure parts of the brain, especially in the region of the tuber cinereum, much discretion must be exercised in interpreting the results of removal. The removal of the anterior lobe seems to show that it is associated with growth development, maturation, and proper function of the gonads, the mammary glands, growth hormones, and adrenal functions. The posterior lobe alone affects respiration, raises arterial pressure, stimulates uterine contractions, stimulates the digestive system, and has some relation to pigmentation. The intermediate lobe also has some relation to the distribution of pigment granules in pigment cells.

The removal of the whole gland, if this is possible without injury to the brain, has a very decided effect on the body of the animal. Since the operation has been carried out on all classes of animals, the results are quite well known in all the groups. The most striking effects are the disturbances of the other endocrine glands and their functions. The effects on the secondary sex characters, caused by the removal of the anterior lobe of the pituitary in young animals, are quite similar to those caused by the removal of the gonads. In males, there is the same reduction of the size of the secondary sex structures, and the gonads themselves become very small. Similar changes occur in females; the ovaries and their secondary sex structures fail to reach normal size, remaining infantile and undeveloped. Recently materials that react upon the ovaries have been discovered in the urine of pregnant females, placenta, amniotic fluids, and blood. These materials, called prolan A and B, have been isolated and their effects studied. Prolan A acts on the follicles of the ovary; prolan B stimulates the formation of the corpus luteum and the follicle-stimulating and the luteinizing hormone.

Thymus

The thymus gland, known as the throat sweetbread of the butcher shop, is located on the ventral surface of the trachea and is a gland of young animals, since it is very large during the growing periods and shrinks materially as the animal approaches and reaches maturity

(Fig. 261).   It is more closely related to the lymphatic system than
to the endocrines, containing lymphocytes along with typical thymic
cells.   It also contains nucleoplasm in large quantities and must be of
value to growing animals.   Disturbances in the lymphatic system are
often associated with abnormalities or diseased conditions of the
thymus, and it appears to have some relation to the growth of the
skeleton, gonads, and nutrition, although its status as an endocrine has
been somewhat questionable.   The removal of the pituitary has a
decided effect on the thymus.   Some recent experiments that con-
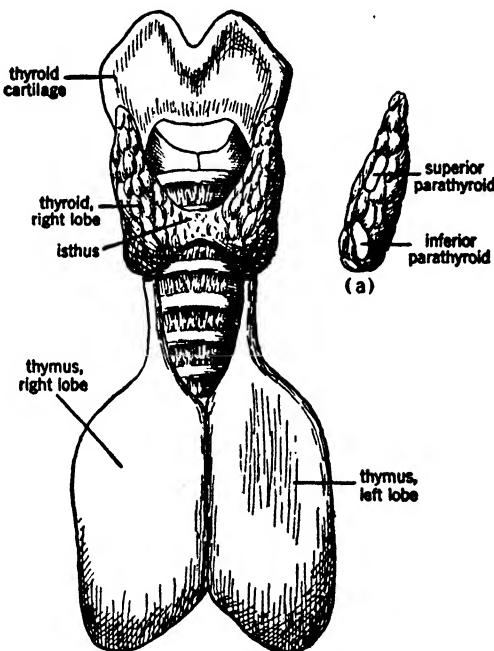
FIG. 261.   Anterior aspect of the human larynx and trachea at birth, to show the
thyroid and thymus, in relation to these structures.   ´ (a) Dorsal aspect of a lobe
of thyroid to show the parathyroids.   (Redrawn from Morris' Anatomy.)

sisted of the removal of the thymus from both parents through a num-
ber of generations showed a definite retardation of the rate of growth
for a time after birth, but later the young approached normal rats
of the same age.   These experiments on young rats and parents appear
to indicate that the thymus of the parents has something to do with the
growth and development of succeeding generations.

The thymus consists of paired glands that take their origin from the
epithelium of the dorsal angles of the gill pouches.   The actual origin
is quite variable, and though the lower forms have them originating

from all the gill pouches, in higher animals their origin is more restricted and usually from the third and fourth gill pouches only. It is probable that the gland is present in the cyclostomes, but it is rather difficult to demonstrate with certainty; in the gnathostomes, however, it is universal in its distribution. In fishes, the thymus consists of a number of glands in a series, along the dorsal angles of the gill pouches. In frogs, the glands are posterior to the jaw and at the posterior, ventral border of the tympanic annulus; in urodeles, they are posterior to the gills. In birds and reptiles, the glands lie along the neck and are associated with the internal carotids, usually being ventral to these vessels. In mammals the thymus extends anteriorly as far as the thyroids, and the posterior end may extend to the base of the heart in young animals.

Thyroids

The thyroids appear to be direct descendants of the endostyle of the protochordates, and are present in all vertebrates (Figs. 261, 262). Originally the thyroids had a duct, which is now lost, and the secretions must be taken up by the blood stream. It is unpaired in fishes; scattered along the branchial arches in the amphibians; unpaired in reptiles and central to the traches; is paired in birds and usually at the base of the bronchii; and in mammals is usually paired and may have a connecting bridge, a condition present in most placental mammals. Whereas the thyroids in the lower vertebrates may be located in different positions along the branchial bars, in mammals they are close to the pharynx and trachea. In abnormal conditions, where the thyroid is enlarged, it may become quite conspicuous in the human, and for this reason it has probably been known for a long time. It is recorded that the Chinese, 150 B.C., recognized the condition and used iodine for a cure.

The thyroids have a distinctive structure, with numerous vescicular cells that secrete a colloid substance containing iodine. In man, the thyroids are quite large, reddish brown bodies that are ventral to the larynx and along the sides of the trachea. There is a large blood and nerve supply. The thyroid is one of the most active of the endocrines, and the results of either hyper- or hyposecretion are quickly apparent in man and animals. The two conditions, however, produce very different effects. Hypothyroidism, or too little of the secretion, causes in young animals a condition called cretinism. The affected individuals remain infantile and never grow up either mentally or physically, since the whole body growth is retarded, including the brain and mentality, and the metabolism is seriously disturbed. Feeding extracts of the gland to young animals in which the supply is deficient relieves the condition to some extent, and there may be an approach to normality,

When the adult lacks the, thyroid secretion, a number of body conditions appear, such as a swelling of the skin, lowered metabolism, and disturbances in the circulatory and nervous systems, a condition known as myxedema. Hyperthyroidism, in which there is too much of the secretion, causes an increased activity as though all the body processes were geared up to an impossible pace, so that the whole body tends to burn out. Because of its accessibility, there has been much experimentation on the thyroid, and it is perhaps as well understood as any of the endocrine glands. There is a very interesting connection between the thyroid and the pituitary, and the thyroid is seriously affected when the pituitary is removed.

Parathyroids

The parathyroids are known in all vertebrates except the fishes, and it is probable that they are represented in this group by some of the epithelial bodies (Figs. 261, 262). Remak discovered them in 1885, and since that time they have always been of interest, although their functions were not known until much later. In 1880, Ivar Sandström worked on the parathyroids and decided that they were undeveloped thyroids. E. Gley, in 1882, found out that their removal caused death through tetany. They came into real prominence through the work of Kohn, who made a thorough study of their anatomy and histology. Much of the information regarding the parathyroids came through a study of the thyroids.

These small bodies developed from the third and fourth gill pouches in man; they are usually four in number and about the size of a bean. They may be on the surface or imbedded in the substance of the thyroid, a circumstance that has led to much confusion and to dissimular results in experimental work, since in some animals they would be removed with the thyroids, while in others the thyroid operation would not destroy them. With a lack of knowledge of the position of the parathyroids, it was difficult to explain why some animals always died after the removal of the thyroids and others lived. Although the parathyroids have not been found in fishes, it is probable that they exist in some form, since the regulation of the calcium supply to the skeleton and to other parts is their function. The first definite bodies that can be classified with certainty appear in the Amphibia, where they resemble small epithelial bodies. They are mesial to the external jugulars in toads and frogs, and are paired on each side, four in all. Urodeles have a similar pair on each side, just posterior to the external jugular. They are present in all reptiles, being located slightly posterior to the thyroids and more lateral, along the side of the neck, appearing as small

oblong bodies usually consisting of two pairs. In snakes, they are closer to the skull than in other reptiles. In birds the parathyroids are usually close to the thyroid and between the jugulars and the carotids, but a few have them on the surface of the thyroid. They may be single or paired, and they have the characteristic yellowish color. In mammals they consist of two or three pairs and are always in association with the thyroids, being either on their surface or imbedded in their material.
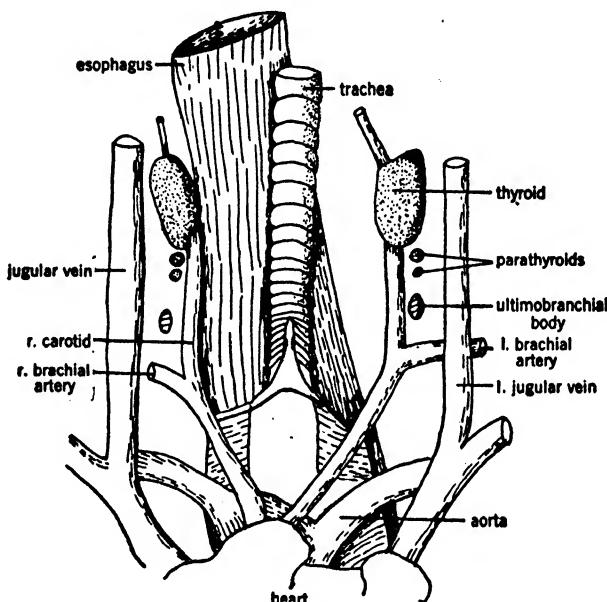
FIG. 262. Blood vessels in the region of the heart in Gallus dom, the domestic chicken, to show associated endocrine glands.

The structure is rather simple, since they consist mainly of a mass of epithelial cells that show some strand and trabecular arrangement, and have colloid between the cells. Their function is the regulation of the calcium content of the blood, and the prevention of the formation of certain substances such as guanidine which appears in the blood after their removal. Their removal results in death in a short time through a disturbance of the calcium metabolism, causing a typical tetany.

Pancreas

The pancreas, a structure present in all vertebrates, is assumed also to exist in the protochordates, perhaps in the walls of the intestine. The pancreas develops as an outpouching from the digestive tract just opposite the diverticulum forming the liver and in adult animals is

usually found in a fold of the intestine just posterior to the duodenum. Its importance as a digestive gland is well known, but was not suspected of other activities until the discovery of Langerhans attracted attention to the interstitial cells, now called the " Islets of Langerhans." The investigations of Banting, Best, and others, in 1921, showed the presence of a hormone named insulin in the pancreas, which is concerned with the regulation of the sugar content of the blood so that a proper sugar metabolism is maintained — a feature very important to all vertebrates. The various distressing metabolic changes, and the loss of sugar through the urine, a diabetic condition, are now very well controlled by the administration of insulin at regular intervals. The medical supply of the hormone is obtained from the pancreas of some of the large domestic animals, commonly slaughtered for food and hence available in large quantities (Figs. 142, 147).

Adrenals

The adrenals or suprarenals are a pair of glands so named because of their relation to the kidneys, since they are always found close to these organs in the higher vertebrates. Each gland consists of two entirely different structures, of different origins, and of different functions in the higher vertebrates. The cortex is derived from the same mesodermic cells that form the kidney; the medulla is derived from the chromaffin cells, the same material used in the formation of the sympathetic system. Fishes and amphibians have the two parts separate, and because of their position between the kidneys they are called interrenals. Reptiles have the two parts closely associated; in mammals, they are enclosed in a single capsule, usually at the dorsal apex or slightly mesial to the kidney (Figs. 323, 324). The adrenals have had a long history, since they were discovered by Eustachius in 1563. They excited little comment or curiosity, however, until Thomas Addison, in 1885, discovered Addison's disease, and associated it with a disorder of the adrenal gland. Epinephrin (adrenalin), the hormone of the medulla, was isolated by Abel in 1900. The active principle of the cortex was first isolated in the years 1929–30, when a number of workers produced the material named cortin, the hormone of the cortex.

In mammals the gland is somewhat triangular in shape, usually forming a cap on the anterior, mesial region of the kidney. It is enclosed in a capsule and is well supplied with nerves and blood vessels. The medulla, darker than the cortex, supplies the endocrine epinephrin; the cortex, lighter in color, supplies cortin. The removal of the cortex causes death, but the removal of the medulla has little effect. After the removal of the adrenals, animals show certain definite symptoms

such as vulnerability to infection, lowered sugar content, and an increase of urea in the blood. The action of epinephrin is striking for its effects in increasing the blood sugar, stimulation of the sympathetic system, and as a check on the action of insulin. The removal causes suffering from heat and cold through loss of temperature control, slow wound healing, and serious physiologic disturbances. Cortin is evidently very important to the body, since the removal of its source causes death. When it is removed there result digestive upsets, lowering of the kidney activity, disturbed sugar distribution, and other physiological disturbances. The isolated hormone is able to keep adrenalectomized animals alive for long periods of time and perhaps indefinitely.

Gonads

Since historic times it has been recognized that the gonads have a decided influence on the body form. Castration has long been practiced, both on domestic animals and man, and its effects were well known, since the secondary sexual characteristics did not appear in animals castrated at an early age. Castration of adult animals causes much less change in the animal body than those performed at an early age. The obvious differences between bulls and steers, roosters and capons, eunuchs and normal men gave concrete evidence of the relationships of the gonads to the secondary sex characteristics. There is some question of the actual function of the interstitial cells of the testes, but it is certain that the testes do contain materials that will modify the effects of castration if transplanted into the castrate animal. The interstitial cells appear to have some relation to the development of the secondary sex characters. A well-known manifestation of the hormone action appears in twin calves, male and female, where hormones of the male so influence the development of the female before birth that it is abnormal, having incomplete sexual organs and being sterile. The condition of this animal, known as the freemartin, appears to be a direct result of the action of a hormone from one animal, inhibiting the development of its twin.

Ovaries. — The gonads of the female carry certain endocrines that are essential to the normal development and physiological functioning of the sex. The removal of the ovaries causes a series of effects that can be changed back to normal if ovaries are grafted back into the body. Male gonads, when grafted in the body of a female, are likely to cause an approach to the male form, particularily the secondary sex characteristics. The pituitary, again, has a decided influence on the female gonads. The product of the Graafian follicle, estrone (theelin), has been isolated not only from the follicles of the ovary, but also from

the liquor of the follicles, the urine, the amniotic fluid, and other reproductive structures. Progestin or corporin is elaborated from the modified follicular cells after ovulation. The action of this hormone is concerned in the events that follow the initial preparation of the reproductive organs for the reception of the egg and the ensuing gestation, decidua formation, and probably other functions. Estrone is concerned primarily in the characteristic changes that occur in the uterine tract, the vagina, and in the behavior associated with the occurrence of oestrus.

Duodenum and Secretin

The first endocrine substance to be described resulted from the discovery of secretin by Bayliss'and Starling in 1906, when they isolated secretin from the duodenum. After physiological experiments they proved that some substance from the duodenum, carried by the blood stream to the pancreas, initiated the flow of the pancreatic juice. From this initial discovery has grown the general idea of the action of hormones, which often influences parts of the body far removed from the gland and the place of manufacture. A second hormone from the duodenum causes the gall bladder to discharge its contents. This product, cholecystokinin, is probably one of several correlating the activities of the different parts of the digestive system.

Ultimobranchial Bodies

The gill pouches are the source of a number of small bodies that have an endocrine function. The ultimobranchial structures are small glands that originate from the fifth pair of gill pouches (Fig. 262). In man they are closely associated with the thyroids and apparently disappear as definite structures. Their history in the lower animals, where they are retained as definite glands, can be followed through from fishes to mammals. They appear as small epithelial bodies posterior to the thyroids, and they have colloidal cells that suggest a similarity to other glands from this same source.

Résumé

Although most of the endocrine glands have been known anatomically since the days of early medicine, their physiology and chemistry are comparatively new subjects. Except for the work of Müller and Brown-Sequard, little was known of their functions until Bayliss and Starling, in 1906, discovered the hormone secretin and coined the name "hormone," or "chemical messenger." The hormone found by them in the duodenum was transported by the blood to the pancreas, where it caused the release of the pancreatic juice. With this start,

the progress of endocrinology has been very rapid, continuing to the present day; it has become one of the most important and productive fields of experimental physiology and zoölogy. The endocrine glands are present in all vertebrates, and it is probable that similar substances exist not only in the invertebrates but also in plants. The amount of endocrine material is always small, since a very limited quantity is necessary for proper action. Although some of the glands have ducts, the endocrine material is carried by the blood stream and moves quite rapidly. The principal glands are the pineal and pituitary of the head region; the parathyroid, thyroid, thymus, the less-known ultimobranchial bodies of the neck region; and the pancreas, adrenals, and gonads of the abdominal cavity. The hormones are specific, and a definite series of effects follows a condition of hypo- or hypersecretion. The hormones developed by one class of animals appear to have similar effects on animals of an entirely different class. The pituitary is recognized as one of the most important of these glandular structures, since it has a decided effect on a number of the other glands of the body. The endocrines are recognized as extremely important in the well-being of the body; their study is of great importance and interest to man; and they are much used in medicine. It is now possible to supply deficiencies or oversupplies, with very good results. A few of the hormones have been made synthetically in the chemical laboratories, but most of them are obtained from animals slaughtered for food, a large and a constant supply of material thus being available.

PART THREE

CHAPTER XIII

FISHES

We study fishes, not only for their own sake, but also because they possess almost all the structural elements from which the characteristic structures of higher vertebrates have developed. Though living in water, fishes have the essential parts that provide a foundation for the growth of organs needed on land. Thus the limbs of tetrapods originated from fins, lungs from airsacs or gill pouches, jaws from gill arches, teeth from scales, and feathers and hair from epidermal appendages, probably scales. It is necessary to go far back into the geological ages to get the starting point in the history of fishes. The earliest true fishes appeared in the Silurian period, and to discover the first fish-like forms would require exploration of even earlier periods. Their primitive ancestors were probably soft-bodied, with no hard parts that were preserved in the rocks; for this reason their traces are difficult to identify. Starting with known conditions as found in the ostracoderms and cyclostomes, we can infer what equipment the primitive forms possessed. From protochordate ancestors they inherited a segmented body, with well-developed myotomes and myosepta, that enabled them to move about on the bottom and gradually assume an active water life. From these early undulating movements fishes developed their characteristic types of locomotion and organization. A definite body shape came with continued movement in a forward direction, and even the earliest forms must have had well-differentiated anterior and posterior ends. The anterior end became specialized as the entrance to the digestive tube with its sensory accessories, and the posterior end became modified and specialized for locomotion. The ancestral fish probably resembled *Amphioxus*. It is possible that the earliest fishes retained a ciliary ingestion and got their food through a primitive sucking mouth, aided by a ciliary tract that conducted the food particles into the gullet. Very early in the history of fishes a new type of mouth was acquired, using the opening of the gills and a part of their skeletal support for the formation of grasping or biting jaws. The sense of smell had been developed early, and now the eyes became an aid in food-getting. A sac-like ear, possibly formed from the lateral line, gave the required sense of balance. Fins as such came after a long period of

time, and it is quite probable that they followed the development of the finfold. (See chapter on skeleton.) The earliest known fishes, the acanthodian sharks of the Upper Silurian, are known from spines, making them the earliest fishes. They had well-shaped bodies, a heterocercal tail, scleral plates around the eyes, numerous spine-like fins, and a persistent notochord. D. S. M. Watson in a recent paper on the Acanthodians, erects a new grade and order the Aphetohyoidea, to include these and some allied forms. This new classification is necessary because of his discovery that there was a complete functional gill between the mandibular and hyoid arches. *Cladoselache* and *Pleurocanthus* are among the earliest known sharks, and they seem to show something of fish ancestry. *Cladoselache* had a terminal mouth, five gill slits on each side, a heterocercal tail, typical teeth, and calcified vertebrae. Its well-defined fins seem to show how these structures were built up by the addition of radials and pterygopodia to the original base. The basal part, however, was still so broad and so closely attached to the body wall as to permit but little movement. *Pleurocanthus*, an elongated shark of the Carboniferous period, was primitive in having a terminal mouth, a diphycercal tail, and primitive fins. It had teeth but seems to have been scaleless. The median fin extended from the anus around the tail and forward to the gill arches.

Many species of elasmobranchs have been able to hold their own in competition with the higher fishes. Modern sharks, representing the end forms of an ancient stock, have lost many ancestral characters and have become highly specialized. They have a world-wide distribution and are very numerous in bodies of salt water. A few species are able to live in fresh water.

Following the great development of the cartilaginous fishes, three groups appeared late in the Devonian period — the ganoids, the crossopterygians, and the lung-fishes. These continue to the present time but are reduced to small numbers.

The term " ganoid " as used by Agassiz originally, included all the fishes with bony plates instead of cycloid or ctenoid scales. As used in a modern sense the term ganoid includes the modern fishes gars, bowfins, paddlefishes, and sturgeons, and their ancient relatives. The ganoids, appearing in great numbers in the Devonian, retained some shark-like characters but developed great coats of armor with peculiar ganoin-covered scales. Because of the hardness of their scales and their suitability for preservation, some of the best-preserved fossil fishes are these ganoids. Their history has been worked out by Agassiz and others.

These ganoid fishes had advanced over the elasmobranchs by adding a number of new characters. The skeleton changed from cartilage to bone by rearrangement of the cells and by deposition of calcium salts.

With this increased stability came a number of skeletal changes, such as the introduction of better ways of joining skeletal elements, and improvements in movable parts. Striking changes took place in the skull, where the cartilaginous chondrocranium became ossified in certain regions, usually around the sense organs, so that it came to be composed of a number of separate elements. The small dermal plates on the outside of the head coalesced and became larger plates that eventually sank in, came in contact with the chondrocranium and became a part of it, forming one structure, the skull. The cartilaginous visceral bars used as jaws in the sharks became encrusted with a number of dermal bones. The palatoquadrate no longer served as an upper jaw but was incorporated as a part of the bracing system of the new structures in the skull. At the anterior end of the skull, two dermal elements, the premaxilla and maxilla, formed the upper jaw line and became the functional upper jaw of the higher fishes above the elasmobranchs. The region of the semicircular canals became broken up into a series of bones which have been associated ever since with ear structures. The attachment of the bony jaw is through a series of bones, the hyomandibular-quadrate chain, which gives much more security and better possibilities of movement. In early forms the gular plates filled in the space between the jaws, but these are now found only in representatives of the older groups, such as *Amia* and *Polypterus*, and in a few teleosts (*Albula*). The surface over the gill region became covered by a series of opercular bones, usually consisting of four, with a secondary series of branchiostegal rays. The pectoral fins were improved by the addition of a number of dermal elements which, together with the ossification of their cartilages, made a much better fin skeleton. The pectoral fins were attached to the skull by a series of small bones, mostly ossifications of dermal elements. The axial skeleton varied, with a growing tendency for the development of better vertebrae and more constriction of the notochord.

This intermediate stock of ganoid fishes started in the Devonian and was once extremely numerous but now is limited to a small number of isolated forms in different parts of the world. The sturgeons have the most extended range, living in a belt around the world in the northern hemisphere. *Lepisosteus* (Fig. 14), the garpike, is found in the eastern half of the United States and extends south to Mexico, Central America, and Cuba. Some of the species reach a length of fifteen to twenty feet in the southern states (alligator gar). The gars are able to compete with the teleosts but live under rather limited environmental conditions. They have not been able to reach the west coast. The spoonbill cat (*Polyodon spathula*) (Fig. 13) is found only in the Mississippi drainage system, and the only other modern representative of the spoonbills

(*Psephurus gladius*) is found in the Yangtze River of China. The bow-fin (*Amia calva*) (Fig. 14) is found generally in swamps and lakes in the Mississippi valley and the eastern states but has not been able to get to the west coast, being rather restricted in the type of water that it prefers.

The crossopterygians include many fossil fishes but only two modern forms, *Polypterus* and *Calamoichthyes* (Fig. 12), both living in Africa. *Polypterus* is found in Lake Tanganyika, one of the oldest lakes in the world, and is very interesting because of its extruded fin-base and the lobed structure of its fin. It is to this group that the student of phylogeny must go to learn something of the origin of the Amphibia. The Osteolepidae, Devonian forms, may be in the line of ancestry, and *Osteolepis* has a number of characters in its skull that have special phylogenetic interest. The crossopterygians approach the teleosts in some respects but have many distinct characters. They are covered with heavy ganoid scales, have a well-developed airsac that can be used for respiration, a notochord that is persistent, a well-ossified skeleton, gular plates, and a diphycercal tail. The fins of *Sauripterus* and *Eusthenopteron*, two fossil forms, have been used as a possible origin for limbs of the amphibian type. The organization of the fins is such that, with some• shifting and rearranging of materials already present, an appendage could be developed that would be suited for holding up the weight of the body in semi-land life. (This will be considered in the chapter on the skeleton.)

The Dipnoi, or lung-fishes, were ,ormerly regarded as ancestral to the amphibians but now are generally considered as being too specialized because of their peculiar dentition and other characters. They constitute an extremely old group distributed over the whole world in the early history of fishes, as shown by numerous fossils. Their skull is covered with bone, but the arrangement of the plates does not resemble closely that of the amphibians. Much of the chondrocranium remains cartilage, and the palatoquadrate has grown fast to the skull and no longer is in line with the upper jaw. The paired fins have a long scaled axis. The spiral valve of the intestines is retained, but the spiracle is lost. The most specialized organ is the airsac, which is highly vascular and is used as a lung when the water becomes low in oxygen content or dries up. There is a return of blood to the heart, the airsac being supplied by a branch of the sixth arterial arch, in contrast to other forms with airsacs in which the supply of blood comes from the aorta (Fig. 277). A partial separation of the atrium has occurred as in the amphibians.

The modern representatives of the Dipnoi (Fig. 11) are found in three very widely separated regions of the world: *Neoceratodus* in a restricted part of Australia, *Protopterus* in the Nile drainage of Africa, and *Lepidosi-*

ren in South America. This great separation of the living forms would supply a serious problem for distribution if nothing were known of the geological history of the group and its former universal distribution. They are able to care for themselves under conditions in which other fishes would quickly perish. *Protopterus* and *Lepidosiren* bury themselves in the mud during drouths and breathe by means of their airsacs, through openings connecting their burrows with the surface. *Neoceratodus* gulps air when the water conditions are not suited for branchial respiration.

The teleosts are highly specialized and very successful fishes, able to live under practically every environmental condition to be found in water, and they have largely replaced the ancient strains in both fresh and salt water. They seem to have evolved at some time in the Triassic period, probably from an old group, the Palaeoniscids; for their type was well established in the Jurassic, and they became fairly abundant during this period. In the Cretaceous they became very numerous, both in kinds and in individual numbers, and took the place which they have held ever since as the predominant type of fishes. They usually are covered with thin scales, either cycloid or ctenoid in shape, but a few scaleless forms are found. There is an extensive bone development, with good organization of the elements of the skull. The occipital region develops a supraoccipital bone, and there is a close union of the dermal and chondral elements. The notochord is reduced to a vestige, and the vertebrae are generally amphicoelous; that is, both ends of the body of the centrum are concave. A homocercal tail is formed by the addition of hypural bones (Fig. 269), and the fins lose some of their radials. A postclavicle series remains, by which the cleithrum and the pectoral girdle are attached to the skull. The gulars are lost, the vomer is single, and the bones of the lower jaw become simplified by a loss of a part of the plates or by the joining of some of the individual bones. A median urohyal is retained. The airsac is purely hydrostatic and is not used for respiration; its duct is permanently closed in most teleosts. The spiral valve is lost and the conus of the aorta is reduced, its place being taken by a muscular bulbus. The testes and the kidneys each have their own individual ducts.

CHARACTERISTIC STRUCTURES OF FISHES

Fishes as a class make up a large part of the vertebrate fauna of the present day, although they are an ancient group that was present at a very early period of the world's history. Their persistence and their diversification prove that they are very well adapted to the environment in which they live. Their many new structures have better fitted them for a more active water life than was possible to their proto-

chordate ancestors. One of their first needs was better locomotion. Developing from a median fold, the tail fin aided in locomotion after the posterior end of the body had been better supplied with skeletal and muscular parts that enabled it to become the main propelling structure. The covering of scales supplied the means of lessening the resistance of the water in their movements and also served for other purposes such as protection against injury.

The many varieties of body shape exhibited by fishes are closely correlated with the particular types of aquatic environment in which they live and with their activities. Sluggish forms that live on the bottom, such as rays, flounders, etc., are flattened or rounded, since speed is no object and their movements are necessarily slow and deliberate. Those that move about freely in the water, either searching for food or escaping from their enemies, have more of the fusiform shape with an approach to proper stream lines. Predacious fishes of the highest type, such as mackerel, trout, salmon, pike, and other fast hunting forms, use every means to develop the highest speed, and these have trim, elongated bodies, well-developed tail fins, and high specializations of the posterior part of the skeleton and its musculature.

An elementary survey of living fishes reveals a most bewildering array of special adaptations and structures, many of which assist them in self-preservation or in food-getting. It is not surprising that these close adaptations should have developed, when one considers the great variety of environments available for fish life. These may be divided into two general classes, fresh water and salt water, each requiring a different physiological balance. In each we find a wide range of temperature and depth. Some are still waters, as in lakes, ponds, and lagoons; others moving waters, with variable speeds, from sluggish streams to rushing torrents requiring a maximum of muscular development. Then there are many varieties of bottom, different kinds of aquatic vegetation, and other changeable conditions. The food of all young fishes and a few adults consists of plankton, the microscopic plants and animals to be strained out of the water by various devices; the adults of most species feed on vegetation, water-living invertebrates, and smaller fishes. The specialized structures of each species should be considered in relation to its particular habitat and its habits.

Scales

The covering of fishes usually consists of protecting scales, except in a few cases where they have been lost (catfish, eels, spoonbill, morays). The scales overlap and form a comparatively smooth covering that

does not impede progress through the water. All fishes are provided with mucous glands in the skin, which pour out their secretion and keep the entire body coated with this slimy material. This not only aids in reducing the friction as the fish goes through the water, but also forms a coating that is resistant to the entrance of bacteria and fungi. The most primitive type of scale is the placoid scale of the shark. It consists of a basal plate with a raised portion that may assume various shapes, usually with several small posterior spines. Scales of this type are always small in size. They are formed in the skin, and consist of a large portion of dentine, a mesodermic material, with a thin coating
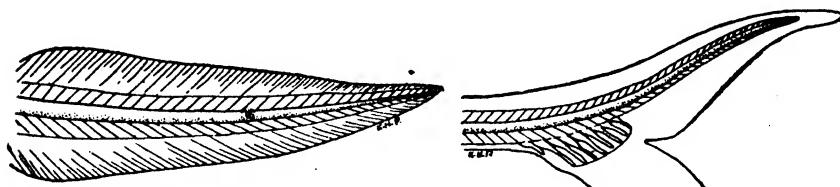
Diphycercal, Pleurocanthus.
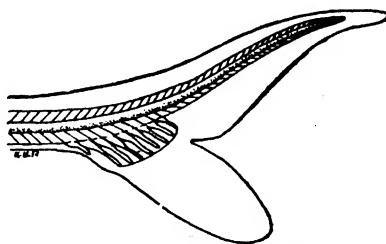
Heterocercal, Polyodon spathula
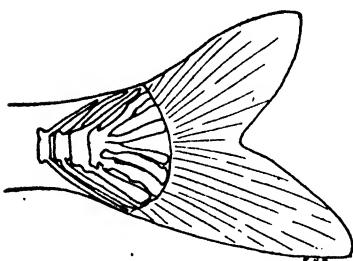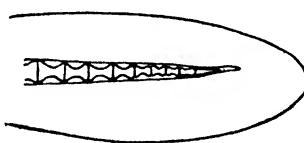
Gephryocercal, Polypterus

Homocercal, Cyprinis carpio

Fig. 263. Types of fish tails. Diphycercal (protocercal) of early shark; heterocercal, paddlefish; homocercal, bony fish; gephryocercal of gars and bowfin.

of enamel supplied by the epidermis. The placoid scale (Fig. 51) is important for the fact that it is supposed to have been the forerunner of the vertebrate teeth, and in sharks it is found that the skin is folded into the mouth during development, carrying these placoid scales along, so that they are in a position to form the teeth. In some sharks there is a graduated series beginning with scales on the outside of the body and ending with teeth inside the mouth cavity. Above the sharks, primitive rhomboid scales, of the " ganoid " type (Fig. 51), appear in older fishes and are found in some modern forms, such as the gars, sturgeons, and surviving crossopterygians. They are rhombic in shape, very heavy and thick, covered with a peculiar substance called ganoin, and

have a complicated structure. They are often fastened together by a peg-and-socket arrangement, so that movement is possible, but they form a rather immobile armor. While very common in the earlier periods, but few armored forms survive today. As the skeleton developed and became better adapted to movement, the scale changed to lighter types, of which there are two, the cycloid and ctenoid. The cycloid (Fig. 51) is found on *Amia*, Dipnoi, and a few modern fishes. It is circular or oval in shape, is comparatively thin and smooth, and does not retard rapid movements of the body. The ctenoid, or the type of scale common to most teleosts, may be circular in outline, except that the free edge has a number of comb-like projections, a characteristic which gives the scale its name. The ctenoid scale varies greatly in shape and size, and is sometimes reduced to small prickles. Scales are replaced when lost, so that the covering always remains intact. They grow by the addition of material to the inner side, each addition being a little larger than the previous one, so that annular rings are formed, made of smaller markings, the circuli. The manner of growth offers a means of determining the age by the counting of the rings of growth.

Axial Skeleton

If the earliest fishes started with an equipment similar to that of *Amphioxus*, it becomes our problem to find out what happened in the way of body changes to bring them to the mechanical level of the shark. The development of the myotomes, or muscle segments, together with the development of a stiffening rod, or notochord, which extended the length of the body, is assumed to have been the first step. The cyclostomes, probably a degenerate group, show slight advances in the organization of the axial skeleton, in that riders, or arches, are formed over the notochord, a rider for each segment. With more use of the myotomes and with the specialization of muscle attachments, these muscle segments came to be highly important and there was the separation of the axial skeleton into segments (vertebrae) to permit a maximum of motion (Fig. 3).

By the addition of material around the notochord, vertebrae were built up, each vertebra being formed from a number of small pieces of cartilage or riders, which were applied to both the dorsal and ventral sides of the notochord. These riders joined together, and, with the final completion of the vertebrae, the notochord was retained only as a vestige, its function being taken over by the perfected vertebrae. The vertebrae of fishes above the sharks are well ossified and have well-

developed processes similar to those of the higher vertebrates. These processes developed to assist in holding the vertebrae together; the anterior process, or prezygapophysis, of each vertebra articulates with the posterior process, or postzygapophysis, of the one anterior to it. The vertebrae also have neural and haemal spines, and processes for the
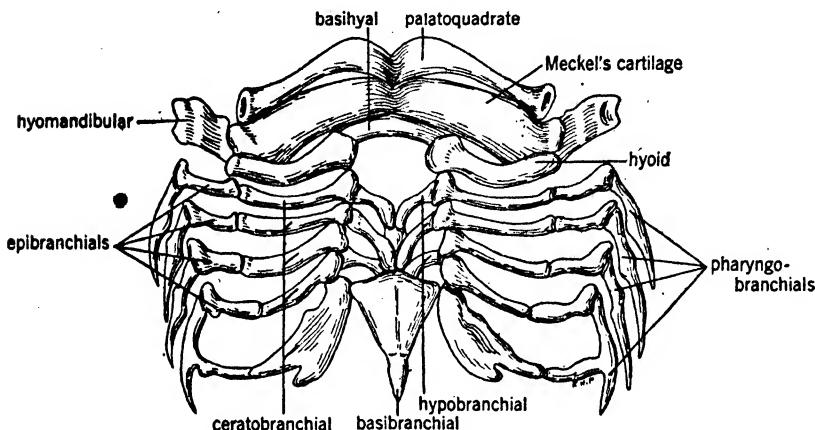
FIG. 264.   Ventral aspect of visceral skeleton of a shark (Squalus acanthias). After Wells.
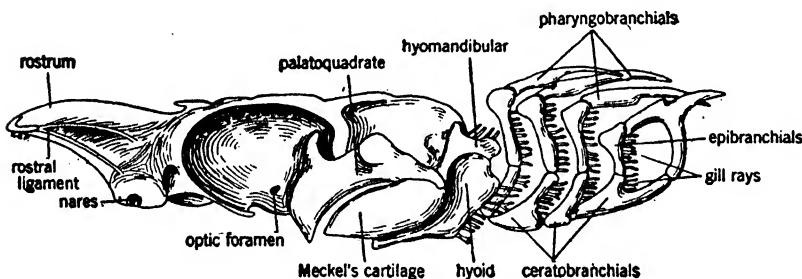
FIG. 265.   Chondrocranium and visceral arches of a shark (Squalus acanthias). After Wells.

articulation of ribs.   The axial skeleton of the higher fishes thus supplies an ample base for the musculature used in swimming.   (See Chapter IV.)

Fins

To prevent corkscrew motions in swimming, some sort of a keel was necessary, and practically all fishes have a fin that serves for this purpose.   Its origin seems to follow the fin-fold theory of limbs (Fig. 110). By the outgrowth of connective tissue into these folds, and by their

connection with myotomic muscles, better movement became possible.
The areas in the pectoral and pelvic regions were enlarged by stress,
but these finfolds served principally as balancers, with only slight use
in locomotion. The tail fin was of the greatest importance as a pro-
pelling organ and assumed many forms. Starting with the perfectly
symmetrical, pointed, diphycercal type, the tail fin developed lobes to
form the heterocercal and homocercal types. Radials appeared in the
fins, strengthening them and making them more efficient. The tail
fin was strengthened first by the addition of horny layers, deposited in
rows, and then by the sinking in of mesodermal plates to form a highly
perfected organ of locomotion (Fig. 263).
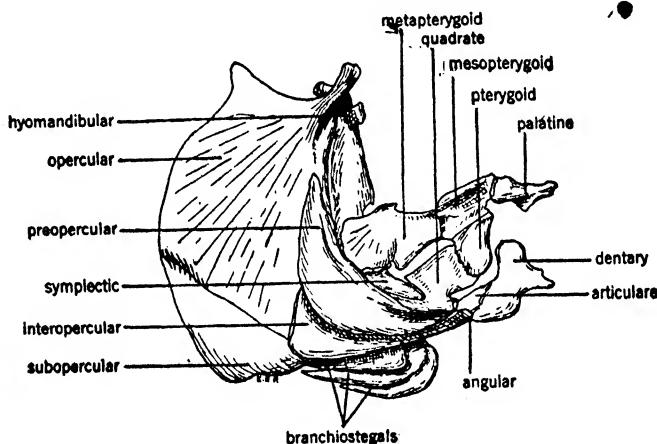
FIG. 266. Right opercular series, pterygoids and mandible of a carp
(Carpiodes carpio).

Paired fins are found throughout most of the fish group. At first
mere lappets (Fig. 113), as in *Cladoselache*, a primitive shark, the paired
fins developed radials, horny rays, and the mesodermic scales that are
drawn in to form the rays of the bony fishes. The paired lappets of
Cladoselache served only as keels (Fig. 113), but in their structure the
framework for the future skeleton of the fins was being laid down. The
paired fins, normally found in the pectoral and pelvic regions, may
shift so that the pelvic pair is anterior to the pectoral pair. The develop-
ment of the cartilaginous bars, as in the shark, gave these fins a special
emphasis and showed something of future possibilities. Pectoral and
pelvic bars, though present in the shark, are not of great importance in
this cartilaginous stage. The paired fins of the Elasmobranchii (sharks)
are rather clumsy structures in the older forms but better organized in
recent types. The supports of the paired fins consist of two semi-

circular bars, the pectoral girdle and the pelvic girdle, to each of which a series of cartilages are attached to form the base of the fins. These cartilages normally consist of a propterygium, mesopterygium, and a metapterygium (Fig. 270). The propterygium articulates with the glenoid cavity, the others form the axis of the fin. To these three cartilages are attached a number of radials, together with a number of small polygonal elements, forming the rest of the fin. Horny cerato-trichia assist in bracing the fins in the shark (Fig. 271). The fins of the higher fishes become simplified in structure, but the girdles become more complicated by the addition of parts in which the cartilage is replaced by bone.
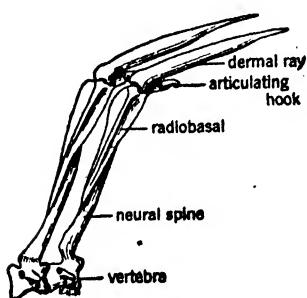
FIG. 267. Bony elements attaching median fin to axial skeleton in a perch.
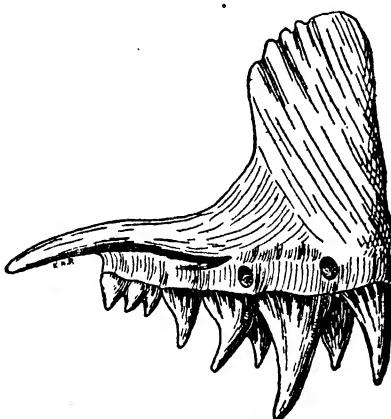
FIG. 268. Right premaxilla of the wolf-eel (Anarrhichthys ocellatus).

The Dipnoi (lung-fishes) developed a biserial fin, with a median axis, a condition rare in the fish series. This type of a fin was used by Gegenbaur to develop his theory of the origin of fins from gill arches. (See Chapter IV.)

The fins of *Polypterus* are extruded by the elongation of the basal parts, so that they have the appearance of limbs. It is from this type of a fin that it is possible to derive the tetrapod limb. In teleosts the basal elements of the fins are reduced or absent, and a few of the radials form the foundation, the rest being supported by a large number of fin rays of dermal origin.

Chondrocranium

The skull of cartilaginous fishes exhibits a certain fixed distribution of parts that is to persist throughout the vertebrates. The importance of the sense organs is indicated by their enclosure in cartilaginous

capsules, close to the nervous system by which they are controlled. The use of the visceral arches as jaws gave the fishes a great advantage over animals that got their food by sucking mouths.

The chondrocranium (Fig. 265) is a box formed of cartilage, which encloses the brain and sense organs. It is supplied with a mandibular arch, of two parts: the dorsal or palatoquadrate cartilage, forming the upper jaw of the shark; and the mandibular or Meckelian cartilage, forming the lower jaw or mandible. A second arch, the hyoid, is posterior to the mandibular arch, which it helps to support. Above the Elasmobranchii, the dermal bones began to form a cover for the cartilaginous chondrocranium, as in the sturgeons. Derived from dermal scales, these bones covered the cartilaginous skull and jaws, and started toward the complete ossification found in the higher teleosts.
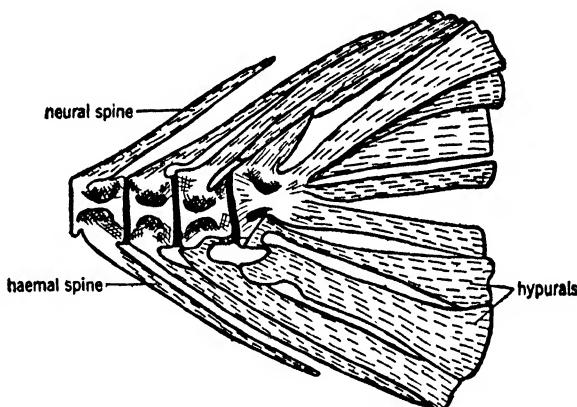
FIG. 269.   Tail of a catfish.

Plates formed around the sense capsules and entered into close relations with the cartilaginous ossifications of the chondrocranium. These plates completed the covering of the brain and built up a series of braces for the jaws. The higher teleosts have a fixed quadrate, braced by a series of bony elements that make powerful jaw action possible. By the complete ossification of the chondrocranium and the sinking in of the dermal bones to join with it, the skull of the teleost was formed. Each of the sense organs was surrounded by a series of bony elements for protection, so arranged as to permit some movement and freedom for growth. The brain thus became surrounded with a structure made up of separate bony elements, with fenestra and foramina to permit the entrance and exit of nerves, blood vessels, and other structures. The region around the gills became highly developed with a series of opercular bones that aided in holding the visceral skeleton in place, and in

supplying the gills with a movable covering. The gill openings were protected by a large opercular, with pre-, sub-, and interopercular bones completing the series. These bones covered the gill slits so that they were no longer exposed as they are in the sharks.

Visceral Skeleton

The visceral skeleton (Fig. 265) of the shark usually consists of seven pairs of arches, the first pair being used for the jaws, the second for the supporting arch, and several vestigial cartilages of uncertain origin being associated with the mandibular arch. A few sharks, such as *Heptanchus* and *Hexanthus*, have more than the normal number.

The mandibular arch is a V-shaped structure, which is joined to the skull by means

Fig. 270. A, pectoral girdle; B, pectoral fin of Squalus acanthias.

of the hyoid arch. Five branchial arches, each with a gill, are attached to this ventral median, hyal series. In sharks, the branchial arch consists of four or more pieces, a ventral basibranchial forming the connecting element.

Fig. 271. Median dorsal fin of Squalus acanthias.

The branchial structures of the teleosts have been changed to bone or replaced by dermal elements. The lower jaw consists of several plates, the dentary, angulare and the articulare, which is the ossified end of Meckel's cartilage (Fig. 266). Other bones may be present in the jaw, but generally the number is not large. The palatoquadrate is replaced by new bones in the formation of the upper jaw and becomes a brace for the quadrate. The new bones, of the upper jaw, the premaxilla, and maxilla, are

of dermal origin, and also articulate with the quadrate through some connecting element such as the jugal or zygomatic. The maxilla of the higher fishes does not bear teeth but serves to form support for the borders of the mouth (see Chapter IV).

Digestive System

The digestive system (Fig. 139) of the fishes may be a comparatively straight tube, rather simple in carnivorous types but variously coiled in the herbivorous, and divided into regions with somewhat indistinct
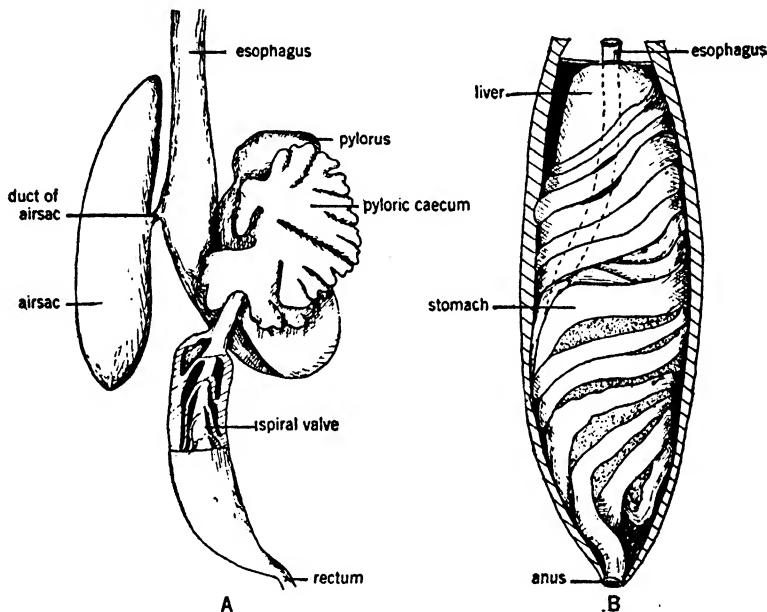
FIG. 272. A, Digestive system of the paddlefish (Polyodon spathula), showing large and peculiar caecum. B, Digestive system of the stone-roller (Campostoma anomalum), in which the intestine is wound around the airsac.

boundaries. The mouth, since it is also used as an intake for water in connection with respiration, is not supplied with glands, for the water would so dilute glandular products that they would be useless. Teeth are generally present, and they have a wide range of form from simple sharp pegs to the highly specialized crushing teeth found in mollusc eaters and herbivorous forms (Fig. 268). The tongue is little developed, since it plays a relatively unimportant part. The pharyngeal region, with its gill openings is provided with gill-rakers and other devices that prevent the loss of food as it goes through this passage. Most of the

water taken in by the mouth is conducted out through gill slits, thus preventing the presence of large quantities of water in the digestive tube. The esophagus is generally long, and there is no well-defined
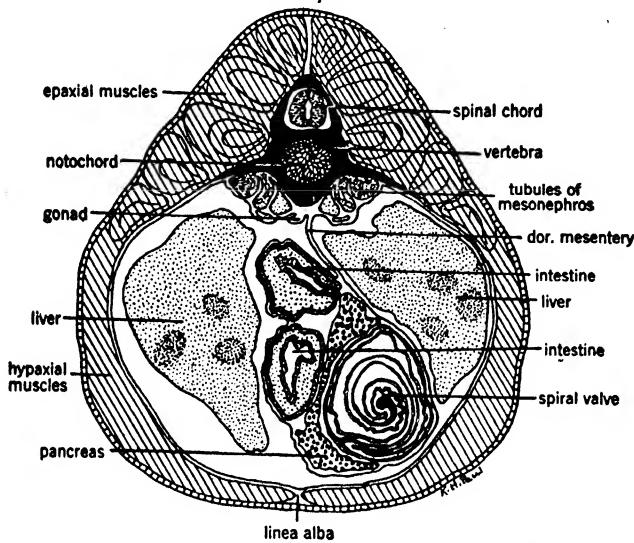
FIG. 273. Semidiagrammatic cross-section of a young Acanthias.

separation from the stomach, since they merge together. The stomach may be divided into at least two regions, the cardiac end joining the esophagus, and the pyloric end joining the duodenum. The lining of the cardiac region is folded; that of the pyloric region is usually smooth and supplied with an entirely different set of glands which distinguish this region. The stomach is usually curved, forming a J-shaped structure in the sharks and some other fishes. The end of the stomach is supplied with a pyloric valve, which leads to the short duodenum. The posterior limit of the duodenum is marked approximately by the entrance of the bile duct, or ductus choledochus, and the ducts from the pancreas. The intestine

FIG. 274. Sphincters around arteries and veins of the stomach submucosa of a ray. After Mayer.

varies from the almost straight tube of the herrings (*Clupea*) to the much-folded intestines of the vegetarian types such as the carp. The intestine is always supplied with glands for digestion, and frequently

with caeca at the pyloric end. The number of pyloric caeca varies from four or five to more than a hundred. The ileum, or spiral valve (Fig. 146), found in the sharks and in the " ganoid " group, is a device for increasing the absorptive area without increasing the length of the intestine. The spiral fold of the ileum is rather closely coiled and is about twenty inches in length, although the total length of the ileum itself is but six inches. Several large arteries carry blood to the intestine and stomach for the nourishment of these tissues and for use in the digestive processes, and large veins carry the digested food to the liver, which acts as a storage place for surplus food material of a certain type. The liver is a large gland filling much of the abdominal cavity or metacoel. A gall bladder and its duct, which supplies the bile to the intestines, is located near the pancreas in the fold formed by the bending of the pyloric end of the stomach and the duodenum. The ducts of the pancreas enter the duodenum close to the entrance of the bile duct. A primitive cloaca is present in the sharks and primitive bony fishes but not in the teleosts (Fig. 2). (See Chapter VI.)

Respiration

Respiration in fishes is carried on principally by means of gills (Figs. 182, 183, 184), specialized structures of the pharyngeal region, so constructed that a current of water bathes them at all times. This water is taken through the mouth (sometimes a spiracle) to the internal gill openings, enters the gill chambers, bathes the gills (Fig. 182), and goes out through the external gill slits. The pharyngeal openings of the gills are usually protected by gill-rakers or some other device to prevent the entrance of food or other débris to the gill chamber. Each gill is strengthened by arches of cartilage or bone, which form a supporting branchial series with additional branchial rays extending between the lamellae (Fig. 182). The two gill lamellae on each arch are thin plates, with a folded surface, in which the branchial blood vessels break up into capillaries, thus bringing the blood in close contact with the water, so that the exchange of gases can take place through the thin, separating membranes. Branchial muscles give movement to the gills so that they can move as the water passes through them. The external gill openings are mere slits in the sharks and lower forms, but in higher fishes, they are protected by a flap of skin or a set of opercular bones, which act as covers. Gills of a different type are found in the embryonic development of some fishes such as sharks and dipnoans, consisting of external filaments that serve in respiration (Fig. 185). Other structures besides gills may be concerned in fish respiration, since in some fishes an enlarged post-branchial pouch, with additional vascular surfaces, enables

them to remain out of water for a short time. These chambers may hold intact a small quantity of water. Above the sharks, an airsac is present, as a diverticulum from the digestive tube, which may be purely hydrostatic, but often respiratory in function as in *Amia, Lepisosteus,* and in the lung-fishes. When used as a lung, it is highly vascular, and provided with a generous supply of blood vessels so that air can be used as a medium of respiration. (See Chapter VIII.)

Airsac. — The airsac of the fishes is considered the origin of the tetrapod lung, and for this reason a knowledge of its history and structure is of importance. The airsac, which is found in all fishes but the sharks and a few bottom-living forms, originates as a diverticulum from the pharynx, and may be a modified gill pouch (Fig. 272). In some fishes its origin is from the ventral side of the pharynx, in others dorsal; and the sac may be either single, as in the teleosts, or double, as in the lung-fishes and crossopterygians. The sac appears in two conditions: (1) a blind sac as in the bass, with the connecting duct closed; and (2) a highly vascular sac that is lung-like in structure and has a duct that opens to the pharynx, as in the lung-fishes, *Polypterus, Amia,* and *Lepisosteus.*

It seems probable that the function of the blind sac is hydrostatic, supplying the fish with a means of regulating the body density. Since the airsac is missing in bottom-living forms, this conclusion seems to be justified. The most interesting arrangement of the airsac is that found in the cypriniform fishes, in which the Weberian ossicles are developed from parts of the first three vertebrae. Typically this mechanism consists of three or four small ossicles arranged in a chain, moved by the pressure of the bladder, and registering this pressure on the semi-circular canals and on the brain, thus forming a natural manometer. The condition of the airsac in the herring (*Clupea*) is interesting, in that there is a posterior opening to the outside of the body near the anus. It would appear easy to fill the sac in this type and also to release it, because of the two openings (Figs. 180, 181).

In the classification of the fishes, the terms *physoclisti* is used for those in which the duct of the airsac is closed, and *physostomi* for those in which the duct is open. Fishes in which the duct of the airsac is closed are supplied with a rete mirabile, a fine network of capillaries in the walls of the airsac, and with gas glands which supply oxygen, carbon dioxide, and nitrogen from the blood. Most of the gas is oxygen, however, and it may be used for other purposes than hydrostatic functions.

A rather limited number of the lower fishes use the sac for respiration, among them the Dipnoi or lung-fishes, the Crossopterygii (*Polypterus*),
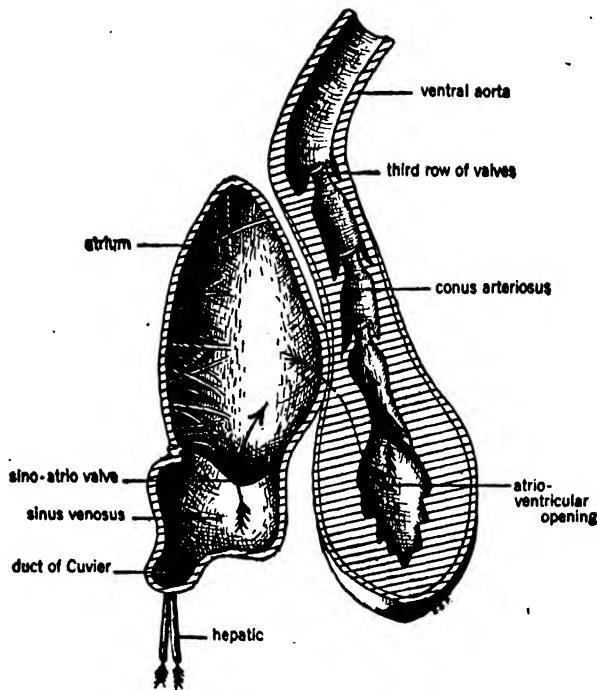
FIG. 275. Heart of a shark.
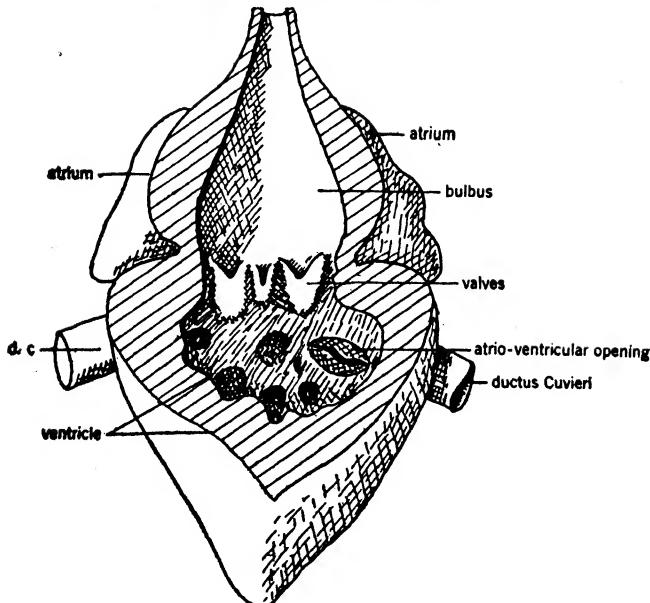
FIG. 276. Heart of a salmon (Salmo salar). After Goodrich.

and the ganoids *Lepisosteus* and *Amia*. In all these the airsacs are alveolar, and lined with blood vessels, so that they can act as accessory respiratory chambers. The airsacs of *Polypterus* and the Dipnoi receive their blood supply from the sixth branchial artery, but in all other forms it is supplied by the dorsal aorta. (See Chapter VIII.)

Circulation

The blood of fishes is of a red color because of the haemoglobin contained in the erythrocytes, or red corpuscles. The erythrocytes are comparatively large and are nucleated. The leucocytes, or white corpuscles, are similar to those of the other vertebrates and always have nuclei. All fishes have a well-developed lymph system through which the body fluids are returned to the blood. The circulation of all fishes may be based somewhat on the primitive, bilateral system of the elasmobranchs, or sharks. In general, the ventral vessels carry the blood back to the heart, while the dorsals carry it to different parts of the body.

The heart, close to the head in fishes (Figs. 275 and 276), consists of two chambers, the atrium, or receiving chamber, and the ventricle, or sending chamber. A single outlet, the aorta, is supplied with pocket-like semilunar valves, to prevent the pushing back of the blood into the ventricle. Coming into the heart, the blood enters the sinus venosus, a loose, thin-walled sac on the posterior side of the atrium. A wide opening, with a pair of valves, connects the sinus and the atrium. The muscular ventricle receives the blood from the atrium through a valved aperture and delivers it to the aorta through a valved conus. The aorta conducts it through afferent vessels to the gills. Teleosts develop a muscular bulbus on the aorta which serves as a compensating structure to prevent too much of a rush of blood through the gills. The elasmobranchs have a number of valves in the conus and have no bulbus. The fish heart (Fig. 151 *A*, *B*) is a one-way structure which receives only venous blood (except in the lung-fishes where there is a small return of blood from the airsacs, with a partial division of the atrium).

Arterial System

The arterial system is the most constant part of the circulatory system. The blood leaves the heart through the ventral aorta and is conducted by capillaries through the gills, where it is separated from the water by a very thin membrane which permits the exchange of carbon dioxide for oxygen. The efferent arteries collect this returning blood from the gills and form the dorsal aorta, through which all the body is supplied. The anterior part of the body and head are served by the

carotids, while the dorsal aorta extends down the body cavity, sending off branches to the different structures and organs. A series of fine segmental arteries supply the dorsal body walls, while the organs receive their supply through single or branching trunks. The aorta diminishes in size until in the tail region it becomes the caudal artery (Fig. 164).
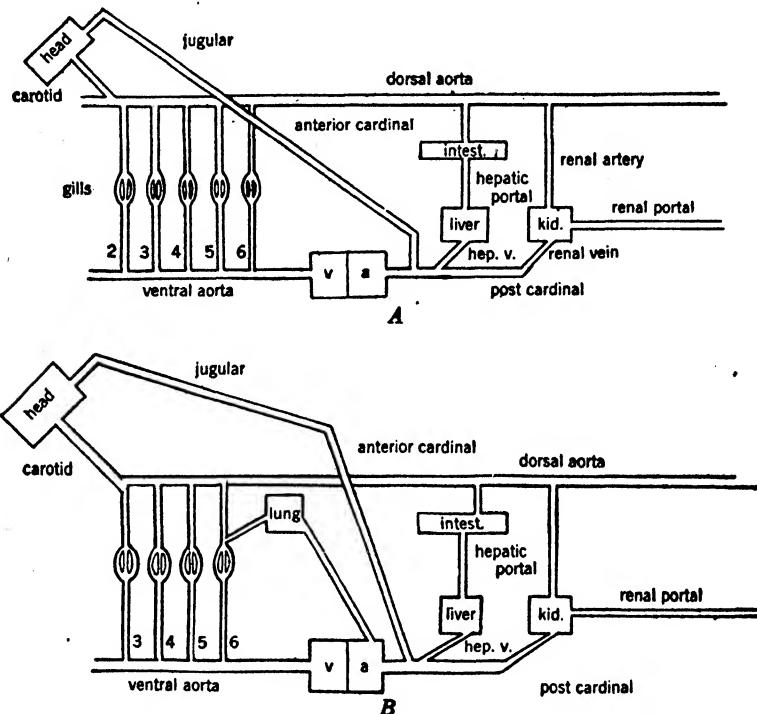
Fig. 277. A, Diagram of the circulation of a teleost. B, circulation of a lung-fish.

Venous System

The arterial system is very direct; the venous system is more complicated and inclined to be more irregular. For convenience, the venous distribution may be divided into several subsystems. Primarily, the cardinal subsystem consists of two pairs of vessels, the anterior cardinals bringing the blood back from the head region, the posterior cardinals bringing the blood from the posterior end of the body. Both of these empty into the ducts of Cuvier and thence to the sinus venosus. The lateral abdominal subsystem returns the blood from the body walls and fins, also emptying into the ducts of Cuvier. The food-laden blood from the intestines is intercepted by the liver, where, after going through

the liver capillaries, it continues through the hepatic veins to the sinus venosus. Glycogen is retained by the liver, for future delivery to the blood as it is needed. Blood from the tail and pelvic regions is collected in a renal portal subsystem, which leads this blood to the kidneys, where it is exposed by the capillaries to the action of the convoluted tubules of the kidney units. Leaving the kidneys, this blood is transferred by the post cardinals to the heart. This is the largest supply of blood received by the kidneys in fishes. Large sinuses are present in the venous systems of sharks, being found in the body, liver, and head regions, but there is a tendency to reduce these in the higher fishes. (See Chapter VII.)

Urogenital System

The nitrogenous wastes of the body, consisting of the end products of proteins and salts, must find a way out of the blood stream other than by means of respiration and the skin, and some organ had to be developed for this function. The invertebrates have nephridial tubes, and a similar structure, but with a different organization, is continued in the vertebrates. Even the segmental character is retained in the cyclostomes, and in the developmental stages of the elasmobranchs. Further development, however, obliterates the segmental structure in the mesonephros of the fishes. The first kidney, the pronephros, consists of simple nephridial tubes, few in number, rarely more than ten and usually less. They have a direct connection with the aorta through small arteries, and pass their products through a pronephric duct to the outside of the body. This structure retains the nephrostomes, which open into the body cavity as in invertebrates. This primitive kidney is in the anterior region of the body and is found in cyclostomes and in the embryological development of all fishes and amphibians. It is functional in these only for a short time, being replaced by a more posterior kidney, the mesonephros, which has many more tubules, usually over a hundred. The segmental arrangement, though apparent in its developmental stages, cannot be seen in the adult. The mesonephros gets its blood supply from the renal arteries, coming off the aorta, and by the renal portal system, which sends the blood from the tail and posterior region around the tubules by means of capillaries. The unit of structure of the mesonephros is a renal, or Malpighian corpuscle consisting of Bowman's capsule, a convoluted tubule, and a collecting duct, which leads the waste to the mesonephric duct and out of the body. The mesonephros lies along the back (Figs. 278, 279), close to the body wall, and is separated from the coelom by the pleuroperitoneal lining. By means of the mesonephros, a part of the blood

is conducted through this filter at every complete circulation. Since this is a continuous process, the blood is constantly being changed by the removal of its nitrogenous wastes. In the male elasmobranch (Fig. 278) the mesonephric duct serves as a vas deferens, and the accessory Wolffian duct, associated with the posterior part of the kidney, carries away the urine, both the vas deferens and the accessory ducts
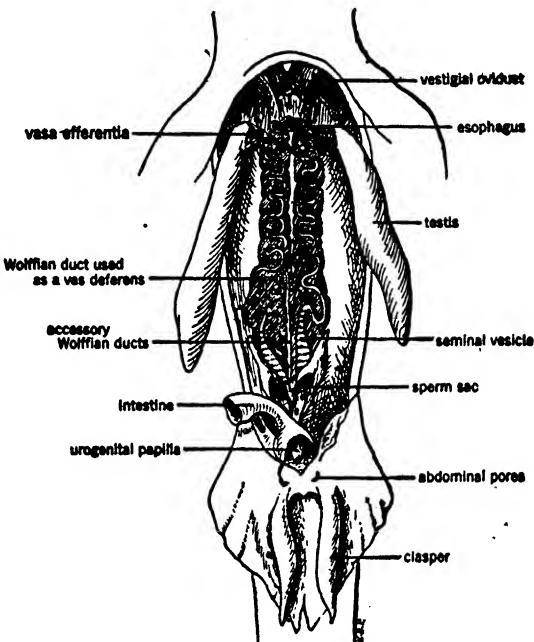
FIG. 278.   Urogenital system of a male shark.   After Goodrich.

having their own openings into the urogenital sinus.   The anterior end of the mesonephros is given over to the reproductive system, carries only spermatozoa, and appears to have nothing to do with excretion, while the distal (posterior) end carries on the process of excretion and is drained by separate ducts.   In the female elasmobranch, the Wolffian duct (Fig. 241) is used only for carrying urine.   It extends along the ventral side of the mesonephros and empties into the urinary sinus.   As in the male, there is a tendency to form accessory Wolffian ducts, and there may be several openings of these accessory ducts into the urinary sinus.

In the fishes above the elasmobranchs, there is a tendency for a greater separation of the ducts, so that the vas deferens of the males is separated from the surface of the kidney and empties into the urogenital sinus by an opening of its own, while the kidneys have their own

ducts and openings. No fishes above the cyclostomes shed the eggs into the coelom to escape through the abdominal pores. Some of the teleosts have a condition that is rather difficult to explain, for in these the ovaries become covered with an ovarial sac, which is continued into the oviduct, so that the eggs are never in the coelomic cavity at all. (See Chapter XI.)
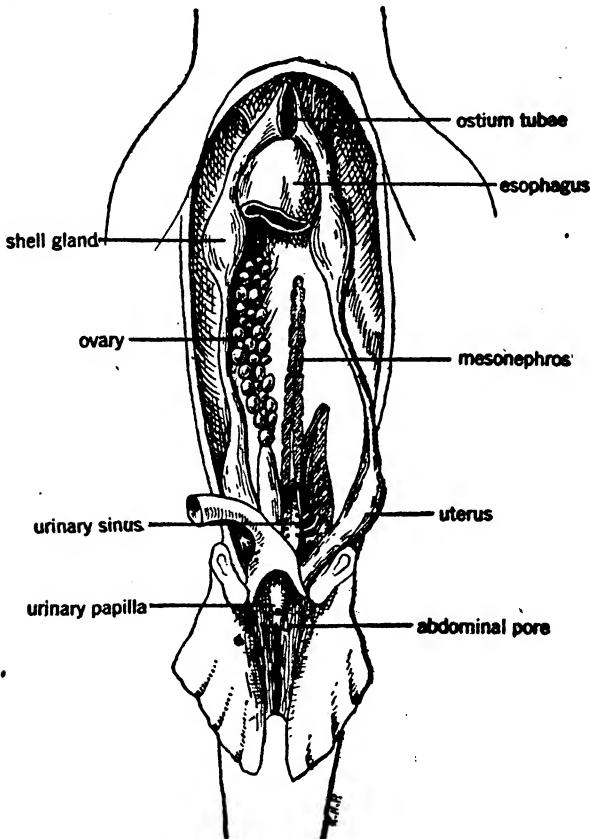
FIG. 279. Urogenital system of a female shark. After Goodrich.

Sex Organs of the Male. — The testes of the male (Fig. 240) are oval, paired structures that lie against the posterior wall of the body cavity, supported by a mesentery, the mesorchium. The testes are made up of a number of tubules in which the spermatozoa develop. Leading from the testes are small vessels, the vasa efferentia, which conduct the spermatic fluid through the mesonephros and into the much-convoluted vas deferens. The posterior end of the vas deferens is enlarged to form a storage sac, the seminal vesicle, and may have a secondary sac for the

extrusion of the spermatic fluid. The spermatozoa are conducted through the urogenital sinus to the cloaca, and in fishes with internal fertilization the pelvic fins may be modified to form an intromittent organ.

Sex Organs of the Female. — The ovaries (Fig. 241) of fishes may be either paired or single, as sometimes one is suppressed. They are usually long and are attached to the dorsal body wall by a mesentery, the mesovarium. In contrast to the testes, they are without tubules for the eggs, and these must escape by breaking through the ovarian wall. The ovaries become prominent when the eggs are developing, and may fill a large portion of the body cavity in the breeding season. The Müllerian duct, or oviduct (Fig. 279), is a long tube which connects the body cavity with the cloaca. The anterior end of the duct forms a funnel-shaped opening, the ostium tubae, which is the entrance way for the eggs from the body cavity in which they are deposited. This opening may be common for the two ducts, or each tube may have its individual opening. The oviduct becomes differentiated into regions, an anterior region in which the eggs are fertilized, an area for the addition of the food material and a shell gland for the deposition of the shell. In fishes that are ovoviparous the duct becomes modified to form a uterus in which the eggs are developed and hatched.

In the egg-laying type, which is the more common, the eggs are fertilized externally. The numbers laid may vary from a few to millions, and of course the mortality is great. Few fishes show any interest in the eggs after they are laid, letting the young shift for themselves. There are, however, some striking examples of parental protection, where the nest is made and guarded. Nests of bass and bluegills are well constructed of pebbles and are guarded from enemies until the eggs are hatched. The familiar stickleback makes a very attractive nest, guarding it with great fidelity. (See Chapter IV.)

Viviparous species are found in most groups of fishes, and in these there is usually some modification of the pelvic fin to serve as an intromittent organ in conducting the spermatozoa into the oviduct of the female.

Nervous System

Following the development of the mouth in primitive fishes, and the added importance of the anterior or head end of the body, there is a concentration of nerve tissue forming the brain. With the mouth are associated the nose, ears, eyes, and other sense organs, and the brain is built up by the addition of nerve material to supply these special structures. The old type of innervation, by means of scattered centers

of reflex action, often practically supreme in the invertebrates, becomes more and more subordinate to the anterior enlargement, and with specialization of the sense structures this overgrowth of the head becomes evident. The early brain might be called a sense brain, but it is more than that even in fishes, for it is of great importance in the coordination of the parts of the body.

The brain of the fish (Figs. 203, 204) is made up of three main divisions: the forebrain, or prosencephalon, which innervates the nose; the midbrain, or mesencephalon, which innervates the eyes; and the
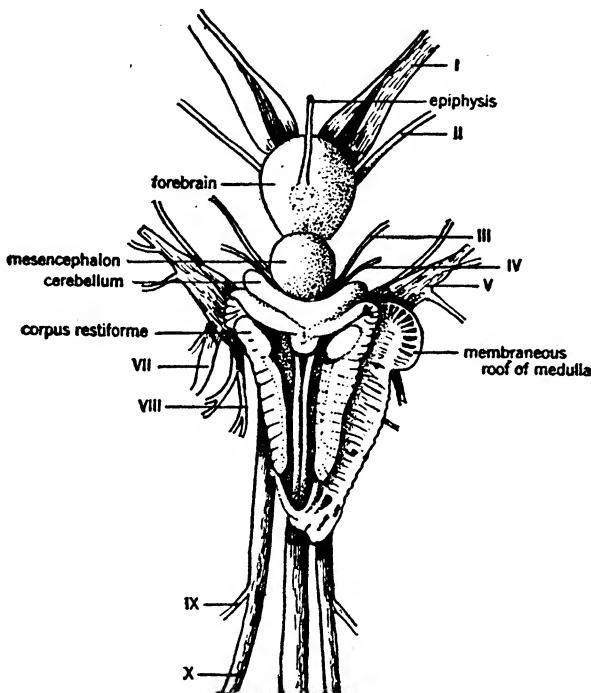
FIG. 280. Dorsal aspect of the brain of Polyodon spathula, with left side dissected away. After Garman.

hindbrain, or rhombencephalon, which innervates the ear (Fig. 280). Both taste and smell were originally very important senses in food-finding. The eye, originally of secondary importance in food-getting, became of more importance as the vertebrates developed. Correlated with improvements in locomotion, there was the development of an organ of equilibrium and coordination, initiated in the cerebellum and connected with its sense organs, the semicircular canals and their ampullae.

With the development of the sense organs and a gradual increase in the need for coordination, there was a corresponding growth of the brain, and it became further subdivided so that in the lowest fishes, the elasmobranchs (Fig. 203), there are five distinct parts that may be distinguished. The *prosencephalon* is divided into two smaller regions, the anterior *telencephalon*, and the posterior *diencephalon*; the *mesencephalon* remains undivided; and the *rhombencephalon* is divided into two parts, the anterior *metencephalon* and the posterior *myelencephalon*. The need of connections and coordinators is evident, for all these senses had to be correlated with movements of the digestive system and with other parts of the body. Even the shark has a brain that is quite complex, made so by the series of necessary tracts and small subcenters. (See Chapter IX.)

The first centers to be considered in the brain are those from which the ten pairs of cranial nerves originate. These centers, beginning as small groups of neurons in the lowest vertebrates and becoming greatly enlarged and integrated in the higher vertebrates, always retain their relative positions and thus are reliable landmarks in the topography of the brain. The development of these centers and their connecting nerve tracts is associated historically with the increasing importance of the organs of sense and locomotion in fishes and their descendants.

The nervus terminalis is an unnumbered nerve which, because of its connections and morphological relations, is now taken to be a part of the olfactory (I). It is small and thread-like, and for this reason was missed by the early workers. First discovered in the Dipnoi, it has been found in practically all vertebrates and is probably universal in its distribution. It arises in the cerebral lobe and extends to the nasal region, where it innervates the nasal membranes. Its exact function is not well understood, but it is probably sensory in character. The olfactory tract, nerve I, leading to the nasal pouches, has its center in the extreme forebrain, or telencephalon, with connections to the motor centers in other parts of the brain. The optic tract, or nerve II, has its center in the corpora bigemina, the prominent optic lobes of the mesencephalon, which are also the centers for the cranial nerves III (oculomotor) and nerve IV (trochlearis), both connected with eye muscles. Nerve VI (abducens) is slightly posterior, taking its exit from the myelencephalon. Cranial nerve V (trigeminalis) is a mixed nerve with a long scattered nucleus that extends through several divisions of the brain and innervates the deeper parts of the anterior head region. Cranial nerve VII (facialis) is a mixed nerve that originates in the myelencephalon and innervates the head and neck. Cranial nerve VIII (auditory), a purely sensory nerve, innervates the sensory structures of the inner ear.

CRANIAL NERVES IN FISHES

No.	Name	Origin	Type	Distribution
	Nervus terminalis	Telencephalon Variable.	Sensory	Mucous membrane of nasal capsule
I	Olfactory	Olfactory epithelium	Sensory	Mucous membrane of nasal capsule
II	Optic	Retina	Sensory	Receptors of the retina
III	Oculomotor	Mesencephalon	Mixed	Ciliary process Superior rectus Internal rectus Inferior rectus Inferior oblique
IV	Trochlearis	Mesencephalon	Motor	Superior oblique
V	Trigeminalis	Myelencephalon	Mixed	Ophthalmicus superficialis: skin of head Ophthalmicus profundus: skin of snout and lateral line Maxillary branch: ventral surface of snout, mouth cavity, region of the upper jaw Mandibular branch: skin of ventral side of head, jaw muscles
VI	Abducens	Myelencephalon	Motor	Lateral rectus
VII	Facialis	Myelencephalon	Mixed	Ophthalmicus superficialis: suborbital canals, ampullae of Lorenzini, lateral line canals Palatine: dorsal region of mouth Buccal: ampullae of Lorenzini, lateral line organs, mouth region Hyomandibular: lateral line Mandibular: lower jaw
VIII	Auditory	Inner ear	Sensory	Auditory regions of brain
IX	Glossopharyngeal	Myelencephalon	Mixed	First gill slit Mouth Hyoid region
X	Pneumogastric	Myelencephalon	Mixed	All gills except the first Lateral line organs Ramus intestinalis to organs of circulation and digestion

Nerve IX (glossopharyngeal) originates in the myelencephalon and innervates the first gill slit and regions of the mouth and hyoid. Nerve X (vagus or pneumogastric) is a sensory and visceral motor nerve originating in the myelencephalon and extending posteriorly to the last four gill arches, lateral line organs, and some of the viscera. In addition to this series of cranial nerves, the brain has connections with the rest of the body through the spinal cord, which is a large tract made up of nerve fibers and reflex centers. (See Chapter IX.)

The spinal cord (Fig. 212) is not only the pathway to the brain for the motor and sensory fibers but also contains reflex centers that act for minor needs and do not connect directly with the brain. It never extends the entire length of the body but grows smaller as it approaches the posterior end; its enlargement as it approaches the brain is caused by the joining of the spinal nerves. Each spinal nerve has two roots, a dorsal root with a ganglion and a ventral root without a ganglion. The two roots join just outside of the cord and then divide into three rami, a dorsal ramus with fibers to the dorsal wall of the body, a ventral ramus with fibers to the ventral wall of the body, and a visceral ramus with fibers to the body cavity and viscera. The visceral ramus is connected with the autonomic or sympathetic system. (See Chapter IX.)

Sense Organs

Sense organs are very important to the fishes in food-finding. The eyes aid those that live in clear water; the nose, with its closely associated sense, taste, aids in the selection of food; and the ear aids in the coordination of muscles used in capturing prey and in keeping equilibrium.

The olfactory organs, at the anterior end of the body, are paired, blind pouches, usually with some device to assure the passage of a current of water through them. (See Chapter X.)

The eye (Fig. 232) is suited for short-distance sight in water. The eyeball can be rotated in any desired direction by means of three pairs of muscles. The lens is spherical, not lenticular as in the higher vertebrates, and the main focal adjustment is by means of the falciform process, which moves the lens slightly forward and backward. Lids and glands are not needed in water. The greatest use of the eyes is in carnivorous forms that hunt their prey in clear water. The optic nerves cross each other to form a chiasma (Fig. 281), but there is no intermingling of the fibers from one eye with those from the other at this crossing point. In higher vertebrates the fibers from the optic nerves split partially at the chiasma, so that those from each eye are conducted to optic centers on both sides of the brain.

The mechanism for equilibrium consists of three semicircular canals in the ear (Fig. 217). Each canal has an ampulla in which there is a papilla with sensory hairs and a connection with the auditory nerve.

The canals are filled with endolymph and have a number of otoliths (small calcareous concretions) which with movement excite the receiving cells on the papillae of the ampullae. By means of this mechanism the fish is enabled to maintain its equilibrium. The sacculus and other parts of the ear, with their sensory patches, seem to be the seat of hearing. Otoliths (Fig. 282) are developed in all vertebrates, most of them being small and micro-

FIG. 281. Chiasma of the optic nerves. A, most fishes; B, herring; C, lizard; D, mammal in which the fibers from one nerve go to both eyes. After Wiedersheim.
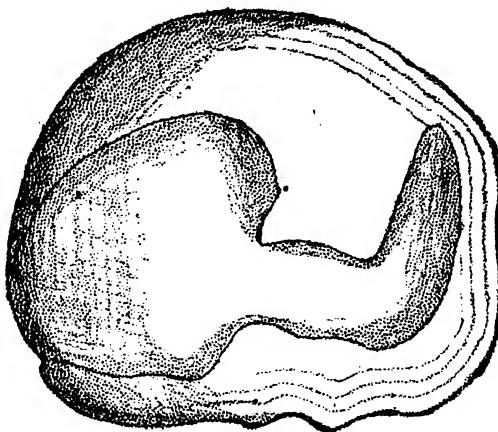
FIG. 282. Otolith of the sheepshead or fresh water drum. (Aplodinotus grunniens.)

scopic, but in some they are quite large. Many teleosts such as the drum (*Aplodinotus grunniens*) develop greatly enlarged otoliths, more than half an inch in diameter. Recent researches have shown that fishes hear much better than was formerly supposed (Fig. 219).

The lateral line, a special development of fishes and amphibians, consists of a series of sensory patches, usually imbedded in the skin, forming lines around the eyes, over the head, and along the side of the body (Fig. 215). The lateral line is innervated in fishes by a branch of the vagus nerve (X). It is supposed to be concerned in the recognition of low vibrations in water. The ampullae of Savi and Lorenzini found in the heads of elasmóbranchs are probably of the same character. (See Chapter X.)

Résumé

Fishes first appeared in the Silurian period and reached their maximum development in the Devonian and Mississippian periods. The ancestors of fishes were soft-bodied animals, somewhat resembling *Amphioxus*; they had a sucking, jawless mouth, with cilia to aid in getting food to the digestive tract. The first sharks had a terminal mouth and lappet-like fins with broad bases, which permitted little movement. The sharks were followed by armored fishes, in which the cartilaginous skeleton was being replaced by bone, and the skull was being covered with dermal plates. Lung-fishes developed an airsac as an aid in breathing. The highest fishes, the teleosts, appeared in the Jurassic, rather late in geological history. Their skeleton typically is almost completely ossified, not cartilaginous. Fish scales are of four types: placoid, ganoid, cycloid, and ctenoid. The pectoral and pelvic fins are in pairs, and there is a variable number of azygous, or median, fins. All have the same structural pattern. The lobe fin of the type found in *Sauripterus* probably gave rise to the tetrapod limb. The chondrocranium is the protective skull built around the brain and sense organs. The visceral arches, migrating forward, formed the basis for the mandibular and hyoid arches. Dermal plates gave the skull its investing bones. The digestive system is short in carnivorous fishes and long and coiled in herbivorous fishes. A spiral valve, which increases the absorptive surface, is present in the lower fishes. The teeth are usually peg-like and are ankylosed to the jaw. The tongue is not well developed. Respiration is carried on by gills, although airsacs may assist, as in lung-fishes. The airsac is present in all but a few bottom forms, and its function is chiefly hydrostatic. Those in which the duct connecting the airsac to the digestive tube is closed are termed Physoclisti; those in which the duct remains open are termed Physostomi. Weberian ossicles, a chain of small bones found in cypriniform fishes, connect the airsac with the nervous system. In the great majority of fishes the blood does not return to the heart after going through the gills, but in lung-fishes there is a slight return of blood directly to the heart. The fish heart consists of two chambers, the atrium and the ventricle, with accessory parts — the duct of Cuvier, the sinus venosus, and the conus, or muscular bulbus. Waste material is removed from the blood by the mesonephros, or kidney. The glomeruli of the Malpighian corpuscles are supplied with arterial blood, but a large amount of blood comes through the renal portal system and passes into the capillaries around the tubules of the mesonephros. In males the spermatozoa generally escape from the body through the Wolffian duct, but in females the excretory and reproductive ducts are separate, the oviduct, or Müllerian duct, carrying the eggs to the outside. Fishes are usually oviparous, laying eggs that are fertilized in the water, but some are viviparous, their eggs being fertilized internally. The brain of fishes is composed of five divisions and is very small in proportion to the size of the body. Those parts of the brain associated with the sense organs are comparatively large. The normal number of cranial nerves is ten. The sense organs, adapted for water use, operate only at close range. Lateral line organs are always prominent.

CHAPTER XIV

AMPHIBIANS

The first land vertebrates were amphibians that made their appearance in the Devonian period when great changes were taking place on the surface of the earth. A single footprint about four inches long, of *Thinopus antiquus*, is the earliest known track of an amphibian. The Devonian oceans were subject to much shifting, as new land areas were pushed up, so that extensive bogs, swamps, and marshes were formed. This changing character of the environment presented difficult problems to the animals accustomed to living in water areas. Many of the marshes dried up by a slow process, and the swamps became stagnant and were filled with dense masses of vegetation. The constant filling of the smaller areas of water and the exhaustion of their supply of oxygen made them less and less suitable for animals with gill respiration. Fishes with open airsacs could live where others were not able to endure the new conditions. While some fishes had become too highly specialized to survive, others were able to adapt themselves to these conditions, but a new system of respiration was necessary for the animals that were to survive on land.

The lobe-finned crossopterygians were not highly specialized and consequently had lost nothing that might be needed later. They already had characters that made them able to adjust themselves to new conditions. The airsac was connected with the gullet by a large tube and had an ample blood supply; its interior became alveolated and filled with small chambers supplied with capillaries, thus increasing the facility for the exchange of gases. The hard, scaly coat of these early forms, though making them rather unwieldy, prevented the rapid drying of the skin, and with a little adjustment it enabled them to make short excursions on land, from one water-hole to another. The skeleton, since it was already ossified, provided the necessary support on land. The fins, with their narrow, extruded bases, were of value in these first overland trips. The plan of the fin was such that, by slight modification, it could be made to bear some weight. Since the modern *Polypterus* uses the fin in this way, it seems probable that the early forms did likewise. The fin rays would have to be shortened and the elements simplified and improved, to make land progression possible.

With the utilization of the airsacs and the eventual obliteration of the gills, there must have been a reorganization of the whole circulatory system, starting with the heart. The atrium had to be divided into two chambers, one to receive the blood from the venous system and one for the blood from the gills. Similarly, the ventricle must either divide or develop a system of valves in the aorta that would prevent the mixing of the venous and arterial blood. (This system of valves is shown by the frog.) The nervous system must follow in the improvement, since land life demands more activity and more coordination of parts. The sense organs had to change to the land type, but these adjustments were not great, since minor changes would make the sense organs of the fish suitable for the new environment. It was necessary to change the nose so that currents of air could be drawn over the sensory hairs, and the eyes had to accommodate themselves to air conditions by added lubrication and by mechanical adjustments that would permit better focusing and a longer range of vision. In the ear the region devoted to hearing was enlarged, and there was a corresponding increase in the related brain centers.

The first amphibians were the Stegocephalia, having heavy skulls resembling those of fishes, and numerous bones that were lost by later vertebrates. They retained a pineal eye, found nowhere else in the amphibians. The pittings on their skulls indicate the closeness of the covering bones to the surface and also the presence of lateral-line canals. The hyomandibular had become the stapes, and there was an opening out of the auditory region to make more room for the added parts of the ear. The palate had large teeth, often with a complicated enamel pattern. The vertebrae retained more of the notochord than the modern forms and had a peculiar structure. True to their fish ancestry, many of the stegocephalians were scaled. They varied in size from *Eryops* (Fig. 16) and the labyrinthodonts, nearly ten feet in length, to the small microsaurs and branchiosaurs, no larger than modern salamanders. This early group persisted down to Triassic times, when it disappeared and was replaced by modern forms.

The Gymnophiona (Fig. 17) are limbless, snake-like amphibians now living in tropical regions. Nothing of their past has been found as yet in geological records. The skull is suggestive of the stegocephalians in its roof architecture. Parts of their structure are rather primitive, but it is probable that their peculiar condition is secondary.

The Urodela have not gone very far beyond the stegocephalian conditions, and their ancestry probably leads back to some of the many branchiosaurs that preceded them. *Lysoropus*, one of the first urodeles known, appears in the Permian of North America. *Hylaeobatrachus*

of the Wealdon of Belgium is another early representative. All the modern groups of the urodeles have been differentiated since Cretaceous times. They are widely scattered geographically, being found on all the large land masses and many islands.

The Anura first appeared in the Jurassic, a number of early forms being known. They seem to have been a branch from the Rhachitomi, to which *Eryops* belonged. The body was shortened in these animals and developed a number of skeletal peculiarities, becoming quite different from the numerous elongated forms that are so common in the group. *Cacops* (Fig. 16), a peculiar little Permian amphibian, was very toad-like and is possibly ancestral. The Anura are divided into toads and frogs, but the structural differences between them are not great.

Ambystoma

Ambystoma tigrinum (Fig. 18), one of the salamanders, is used as an example of the amphibians, since it occupies an intermediate position in the class, living both in water and on land. The Ambystomidae have much in common with the branchiosaurs, which were among the last of the stegocephalian groups to die out. The members of this family are very common in the United States and America generally, with a few species in India and in other parts of the East. Their eggs are laid in water, early in the spring, and the young normally pass the summer in the water, but they may spend many years as larvae or never metamorphose. *Ambystoma tigrinum* is unique among vertebrates in that it develops sexually and is able to breed while in the larval stage (neoteny). The axolotl, or immature stage, of this species was originally described by Dumeril in 1866 as a distinct species under the name of *Siredon pisciformis*, for it was mistaken for a mature form, and its identity was not suspected until some specimens that had been taken to Europe were found to have transformed.

After transformation, the adults leave the water and live in damp places, feeding mostly on insects. They hibernate by getting into some protected place, where they can be damp and avoid freezing. They are frequently found in cellars, cisterns, rocky ledges, or under piles of damp material. They wander long distances and may be found far from water in this stage.

Skeleton. — The skeleton of *Ambystoma tigrinum* shows many adjustments to land life and is much simplified, since numerous fish-like characters have been lost. The limbs and girdles (Fig. 284) are of the tetrapod type, consisting of fewer parts than are found in fins. The axial skeleton is more compact, and the vertebrae are smoother and of

more solid bone. The lateral line, so prominent in the stegocephalians, has been reduced. The skull (Figs. 78, 79, 283) is striking for its compactness, in contrast to the loosely knit skull of most fishes. There is a great reduction of the number of bones, since many of the fish elements have been combined with others, changed in function, or entirely lost. The jaws, instead of being loosely articulated to the sides of the skull as in fishes, appear to be an integral part of it. The nasal and oral regions are much simplified by the loss of many small elements. The hyomandibular becomes the stapes, or the basal plate that fits snugly into the foramen vestibuli of the middle ear. The pterygoid series is reduced to one or two elements, which still aid in tying the
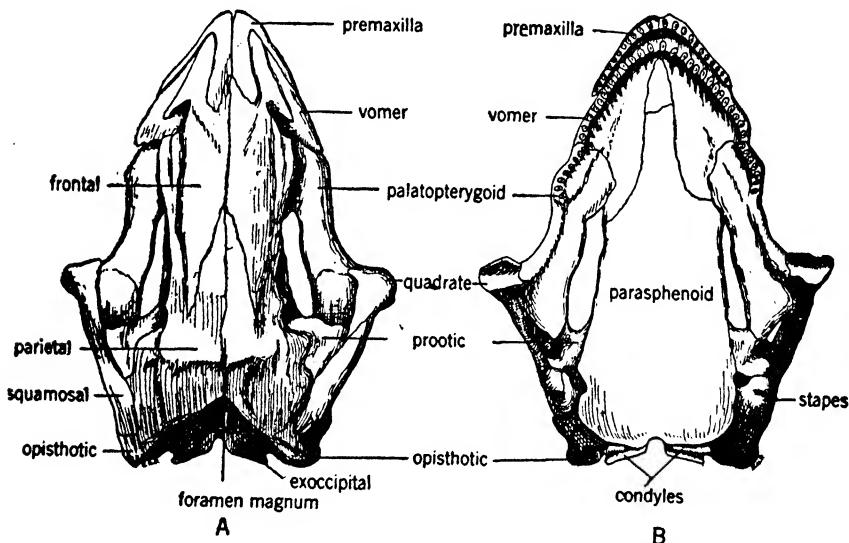
FIG. 283. Skull of Necturus: A, dorsal; B, ventral.

quadrate to the skull but in a much more stable manner than in the fish. The squamosal now joins the quadrate directly to the skull. The brain case is practically surrounded by bony elements, the sphenoids on the sides being either cartilage or bone, but filling in the anterolateral space not covered in the fish. Two occipitals are formed surrounding the foramen magnum, with a condyle on each for the articulation of the cervicals. The parasphenoid of the fish is retained as an extensive element in the roof of the mouth. Most of the series of bones that covered and supported the fish gill arches are lost, and those that remain have become a part of the hyoid series, for the support of the tongue and throat musculature, and have contributed material for the laryngeal structures.

The axial skeleton is consolidated, the parts reduced, and the vertebrae better formed, losing their vacuolated appearance and roughness. All the series of bones that supported the median fins are gone, and the neural spines are smaller in proportion and shorter. The vertebrae are better locked together by pre- and postzygapophyses. There is a suggestion of the breaking up into regions and further differentiation of the spinal column. The vertebral column shows some specialization in the pelvic region, but the fine differentiation found in higher vertebrates is lacking. *Ambystoma* has a series of ribs extending along the body, but they are generally short and of little importance. The single cervical vertebra has no rib.

The most striking development is shown in the limbs, which are of the definite type found in all vertebrates above the fishes. The stegocephalians retained some of the fish-like bones in the pectoral region, but none of these are found in modern amphibians. The anterior, or pectoral, girdle consists of an ossified scapula, cartilaginous suprascapula, and ossified coracoid. The posterior girdle also consists of three parts: an osseous ilium, connecting with a sacral vertebra; an osseous ischium, bracing the ventral part of the girdle; a cartilaginous pubis, with no ossification.

Fig. 284. A, right shoulder girdle of Necturus. B, sternum of Rana.

The plan of the forelimb (Fig. 117) is that of the tetrapods, consisting of the following parts: a single proximal element, the humerus; a radius and ulna forming a forearm; a carpal series of three elements, the ulnare, intermedium, and radiale; a median centrale; and a series of distal carpals (1, 2, 3, 4) articulating with the metacarpals; the four digits completing the manus. If five is the original number on the hand, one digit has been lost (Figs. 102, 114, 115, 123).

The posterior limb is of the typical tetrapod type, with the following parts: a single proximal element, the femur; two elements in the
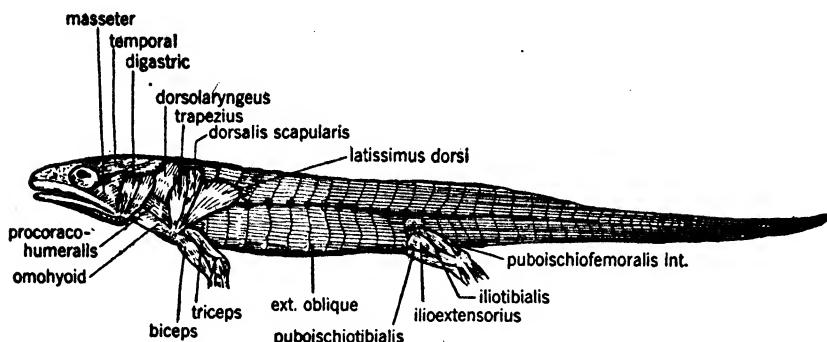
FIG. 285.　Lateral musculature of Ambystoma.

second segment, the tibia and the fibula; a tarsal series, the tibiale, intermedium, and fibulare; a centrale; a distal series, consisting of tarsale (1, 2, 3, 4, 5); five metatarsals; and five digits (Fig. 117).

The girdles (Fig. 102) are weak, and the limbs, extending out at right angles, do not properly support the body in walking. This condition of the limbs is somewhat improved in the reptiles, but it is not until the birds and mammals are reached that limbs have a position under the body, where they are mechanically most efficient for support.

Musculature.—The myotomic musculature is retained, showing very clearly along the side of the body (Fig. 286). The series of muscles connected with the skull, jaws, and visceral

FIG. 286.　Ventral musculature of Ambystoma.

arches are decidedly changed, principally in shifts of origins and in-

sertions, and in the splitting of massed muscles, so that they are better able to serve the movable parts. Each limb has its specialized musculature, because of the many new parts and the very different use of the tetrapod limb. With this more complicated musculature is associated a change in the nervous system and an enlargement of the motor centers, so that more exact coordination is possible. It also implies new connections with the cerebellum and cross connections for the coordination of the movements of the muscles of the two sides, since equilibrium is one of the necessary developments of land life (Figs. 285, 286).
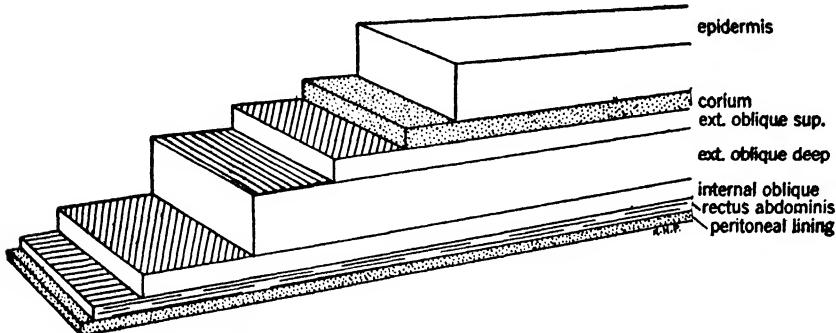
Fig. 287. Diagram of the layers of the body wall in Ambystoma.

Dermal Covering. — The ancient stegocephalians were scaled, and the Gymnophiona, one modern division of the amphibians, have scales imbedded in the skin, but all the others are scaleless. The skin (Fig. 49) is modified in the toads with warts and excrescences in preparation for land life, but in the rest there is little skin adaptation. The great problem of all amphibians is to prevent excessive evaporation of moisture through the skin, but at the same time the skin is used as a secondary organ of respiration and for this reason is filled with capillaries. A regular blood supply is sent to the skin through the cutaneous artery, and this is very important, since the lungs are inadequate to give sufficient area for the interchange of gases. Mucous glands in the skin help to preserve the moisture. Since life on land demands a skin that will prevent evaporation, there is an outer skin, or epidermis, but it remains alive, and is not covered with dead cells as in the reptiles and the higher vertebrates. The color is fixed by chromatophores present in the corium, and while change of color is possible, it is rather limited.

Digestive System. — The digestive system (Fig. 288) of *Ambystoma tigrinum* is rather simple, as in all amphibians. The oral cavity is different from the fish, in that it has an opening into the nose. The

teeth are just large enough to make a slight roughness on the bones where they are located. There is no need of very large teeth, since the food is mainly insects and worms. The tongue is small, fixed to the floor of the mouth, and has very little ability to move. A small glottis, slit-like in form, marks the opening to the trachea. The esophagus is short, opening into a long, spindle-shaped stomach, the lining of which is thrown into deep folds, showing little of the lumen in cross-section when empty. The spleen is closely applied to the left side of the stomach. A short duodenum receives the bile and pancreatic ducts. The small intestine is short, with about six loops between the duodenum and the cloaca. The intestine also has the lining folded but not so deeply as the stomach. The anal opening on the anterior, dorsal side of the cloaca, is large in comparison with the entering intestine. The digestive processes start in the mouth aided by a number of glands heretofore lacking, which supply enzymes and keep the mouth moist. The liver is large, consisting of several lobes, with a well-developed gall bladder, and covers the stomach on the ventral side. The pancreas is placed in a U-shaped bend between the stomach and the duodenum, and empties into the duodenum close to the choledochal duct. (See Chapter VI.)
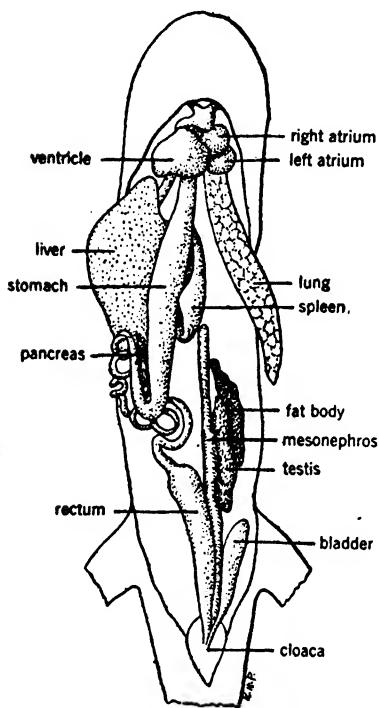
FIG. 288. The viscera of Ambystoma.

Respiration. — The two lungs (Fig. 288) are thin-walled, alveolar sacs that extend posteriorly almost half the body length. From the glottis, the trachea extends posteriorly a short distance, before dividing into bronchii. The alveoli are shallow and do not supply sufficient surface for respiration without the help of the skin with its large cutaneous vessels.

Circulation. — The blood in amphibians, as in fishes, consists of straw-colored plasma with large, oval, nucleated erythrocytes, or red corpuscles, and large lymphocytes, or white corpuscles.

The circulation of the amphibians responds to new conditions by

dividing the atria, developing a cutaneous system as an accessory, eliminating parts of the aortic arches not needed with lungs, and beginning the replacement of the paired posterior cardinals by the new *postcava*. In the adult form of *Ambystoma* and other urodeles the gills are lost and the gill slits permanently closed. The position of the heart (Fig. 288) is very much anterior, being partly between the jaws. It consists of right and left atria, a single ventricle, an aorta, and four aortic arches. An almost perfect septum divides the atrium into two chambers, thus making a three-chambered heart. The right chamber receives the blood from the venous system and the left from the lungs. The atria open into the single ventricle through a slit protected by a valve, so that there can be no return of blood under pressure from the ventricle. Since blood from the veins and lungs flows into the same receptacle, the ventricle, some arrangement, mechanical or otherwise, must direct the blood to its proper channels, the venous blood to the lungs and the aerated to the systemic vessels. Both the atria open at the same time, with an instantaneous contraction of the ventricle following. The venous blood is close to the first outlet, the pulmonary arteries, and goes there because it is the easiest and the most direct path to follow. The last part of the contraction of the ventricle (systole) sends the arterial blood through the systemic arch (arch 4) and carotids. A vestigial fifth arch is retained in the urodeles but lost in the Anura. The bulbus, a muscular enlargement of the aorta, assists in the regulation of the blood after leaving the heart. This muscular bulb is capable of distension, swelling with every beat and thus preventing any back pressure on the heart. The old aortic arches (Fig. 160) have been remodeled and connected so as to form an arterial path with no intervening gills. The division of the ventricle is suggested in the amphibians by the incipient division of the aorta into two separate vessels. The arterial system (Figs. 165, 166) is direct and resembles that of the shark in its general plan, being modified only as much as is required by
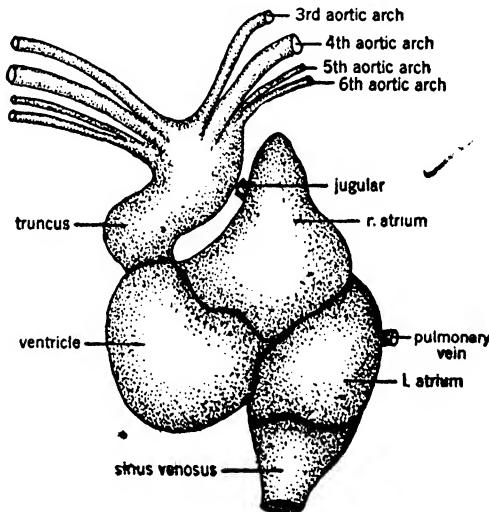
Fig. 289.   The heart of Ambystoma.

the mechanical demands resulting from the elimination of the gills and the addition of the cutaneous system (Fig. 290).

Venous System. — The venous system in amphibians (Figs. 171, 172) is like that in fishes with modifications to new conditions. The anterior cardinals are retained for the return of the blood from the head. The duct of Cuvier is retained also, because it is useful in gathering the blood from the two sides and delivering it to the sinus venosus. The system is still fish-like in its bilaterality, and the eventual shift to the right side of the body is only suggested by the condition in the Amphibia. The post cardinal system is functional in the urodeles, but a new vessel, the postcava, is appearing, that is to replace them in the Anura, toads and frogs, and continue in all the higher vertebrates. The post cardinals return the blood from the kidneys and the posterior end of the body, delivering it to the duct of Cuvier. The lateral abdominals,
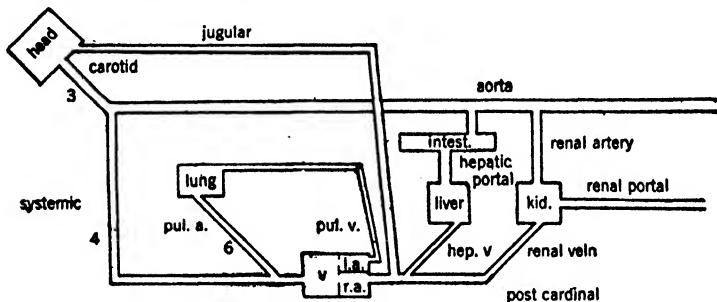
FIG. 290. Diagram of circulation in a frog.

paired in fishes, now unite and continue to the heart as a single vessel, with new connections to the renal portal system, to which it delivers a part of its blood. The caudal system is fish-like, delivering its blood to the mesonephric kidney and retaining its character as a renal portal system.

Nervous System. — The brain of *Ambystoma tigrinum* (Fig. 291) may be taken as typical of the urodeles, with a development only slightly in advance of the Dipnoi. Internally the brain is an advance over that of the fishes, since it is gaining new centers and connections that are to be so important to the vertebrates. The telencephalon is larger and more distinctive, with a development of the pallium in which there is now a slight invasion of nerve cells. The diencephalon, covered by a large paraphysis, is small with a large hypophysis on the ventral side. The small epiphysis or pineal eye is present but does not penetrate the roof of the skull, since there is no foramen for it except in the stegocephalians. The mesencephalon has the two lobes joined, with no dividing line between them.

A decided depression marks the line between the diencephalon and mesencephalon. The cerebellum is not so large as would be expected, but is a tiny bit of brain material forming the anterior border of the fossa rhomboidalis. The myelencephalon, or medulla oblongata, has a deep fossa and the usual nerves coming from its sides. The ventricles are similar to those found in the shark. The large elongated cavities in the lobes of the telencephalon are connected with the third ventricle by the interventricular foramina. The third ventricle is connected with the fourth by a small tube that extends through the mesencephalon to the myelencephalon (Fig. 205).
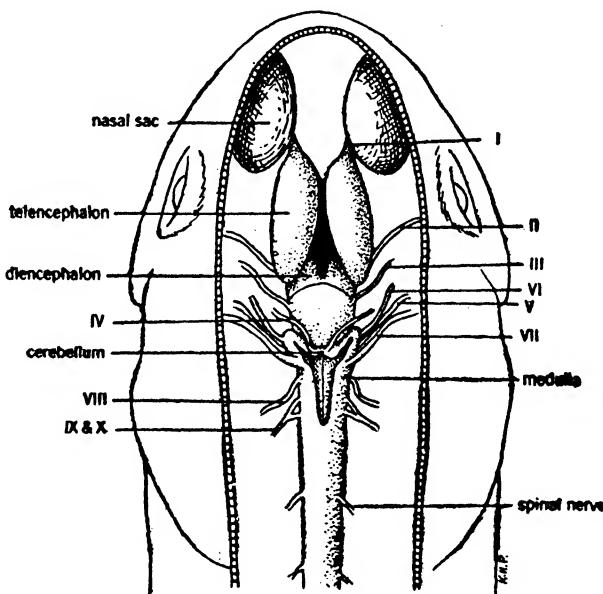
FIG. 291. Dissection of the brain of Ambystoma.

Sense Organs. — The nose is still fish-like in its appearance, being a large sac, but it has acquired a connection with the mouth, the internal nares being situated at the anterior-lateral side. The external nares are small and provided with valves so that they can be closed when air in the mouth is forced down into the lungs.

The eyes show a few changes necessary to land life, in the development of the lids, a better means of focusing the lens, and the development of the glands that aid in keeping the cornea moist. The lens is round as in the fishes. (See Chapter X.) The ear of *Ambystoma* (Fig. 220) is typical of the urodeles and anurans. The middle ear is abortive in the urodeles, and the Eustachian tube is lost. The mem-

branous ear is similar to that of the shark, but there is a better development of the sacculus, which is greatly enlarged and usually contains a large otolith. The lagena is of moderate size and not highly developed. The stapes, a new structure, appears for the first time in the amphibians, forming a plug which is associated with the foramen vestibuli. This rod of bone is buried in the muscles of the jaw in *Ambystoma*, but in *Necturus* it articulates with the squamosal.

The anuran ear (Fig. 221) is quite different from that of the urodele, since the middle ear, derived from the first gill pouch, is present with its opening to the throat through the tuba auditiva. An extra development of the stapes, the extracolumella, lengthens the ear ossicle; and an external membrane, the tympanum, to which this element is attached, catches the sound vibrations.

The lateral line is present in all the amphibians that live in the water, and in the young stages of the land forms. Traces of this structure are found on the skulls of the stegocephalians, as would be expected.

Urogenital System. — The kidney is of the mesonephric type (Fig. 292) comparable to that of the fishes, with nephrostomes retained and opening into the body cavity. The units of structure, the Malpighian corpuscles, number a hundred or more, in contrast to the very small number in the pronephros. The blood supply comes to the glomeruli direct from the aorta as in the fishes, but the renal portal is still retained to bring the blood from the tail and posterior end of the body, where it goes through the capillaries that surround the tubules. The kidney is not in the coelomic cavity, but dorsal to it, and covered by the pleuroperitoneal lining. The mesonephros is an elongate structure, extending from the anterior part of the cavity to the cloaca, to which it is connected by the mesonephric duct. The bladder opens into the ventral side of the cloaca.

In the male (Fig. 292 *A*), the Müllerian duct, although vestigial and of no functional importance, extends to the anterior end of the coelom. The testes are elongate and yellow, each with an attached adipose body. The vasa efferentia take the spermatozoa through the anterior nonfunctional part of the kidney, to the mesonephric duct, which is used as an outlet for the seminal fluid. Only the posterior end of the mesonephros is functional, the anterior end being given over to the transfer of the spermatozoa. The spermatozoa are collected together and ejected in small, white, cone-shaped packets called the spermatophores. These are taken into the cloaca of the female, where the spermatozoa escape and fertilize the eggs.

The female (Fig. 292 *B*) has no connection between the reproductive and urinary systems. The kidney is the same shape as in the male, but
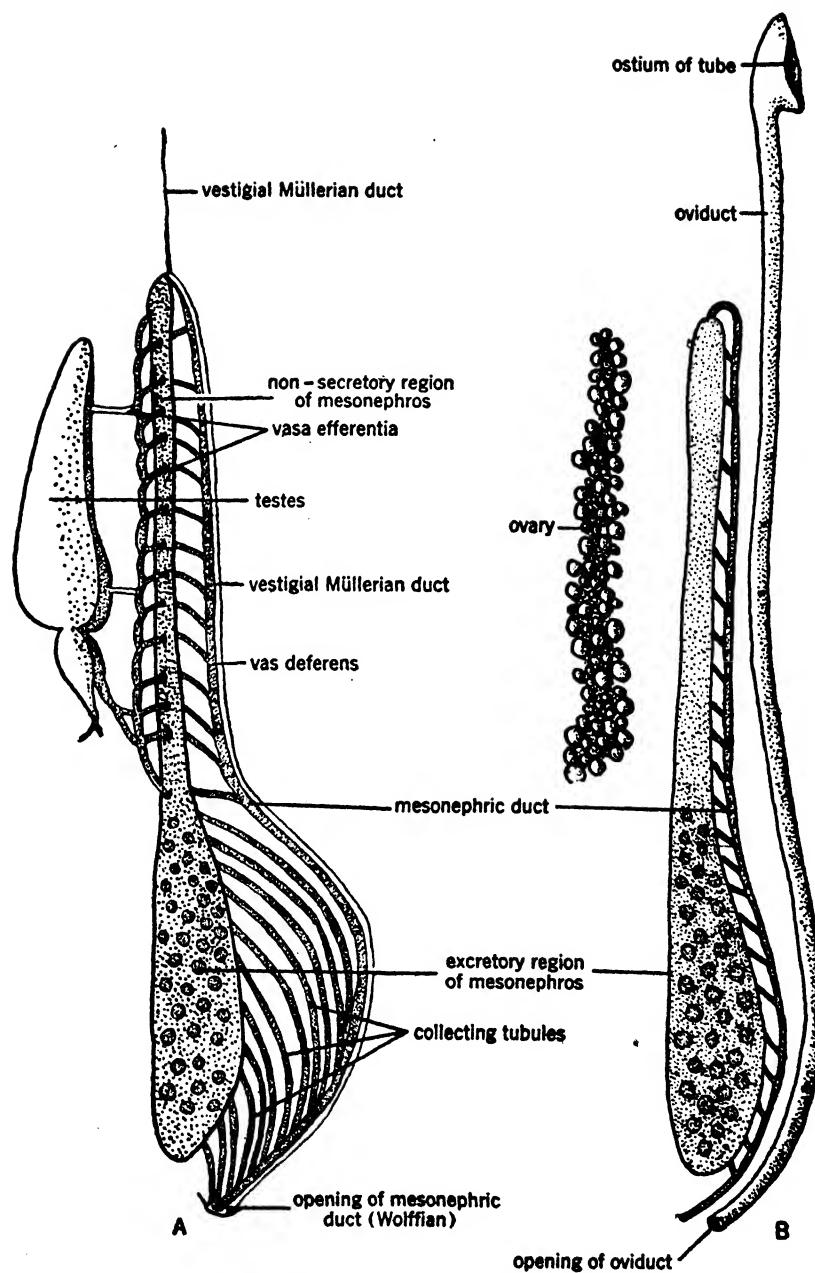
FIG. 292.   Diagram of the urodele urogenital system.   A, male; B, female.
After Weidersheim.

the mesonephric duct carries nothing but the products of the kidneys. The Müllerian duct, or oviduct, extends to the extreme anterior end of the coelom, where it develops into a funnel-shaped opening, the ostium tubae. Through this funnel, the eggs reach the oviduct, and escape through the pores to the cloacal cavity (see Fig. 242 *A, B*).

Adrenals. — The adrenals resemble those of the elasmobranchs in that there is a separation into a cortical (inter-renal) and medullary (supra-renal) parts. They are small in *Ambystoma* and are located along the inner side of the mesonephros with small bodies along the aorta.

Metamorphosis

The Amphibia have never entirely lost their contact with water life, and in reproduction practically all, even those that live on land, go back to the water to lay their eggs. Often this involves much risk and hardship. The eggs are laid in water in different ways; toads lay theirs in double strings; frogs lay theirs in masses; *Ambystoma* deposits them singly on bits of vegetation; and *Necturus* attaches them under bits of wood and under rocks. Most amphibian eggs are heavily pigmented but have a limited amount of food in the yolk. The young hatch in a few days and at first have little of the appearance of vertebrates, since most of the development comes later. The young live on the yolk for a time, finally getting a functional mouth and being able to take other food, usually vegetable matter. The growth continues, and the larvae now resemble a fish with three external gills, which serve in respiration. The organization of the muscles is fish-like, with evident myotomes and a tail used as a propeller. The fish-like circulation is retained in those that remain in water, but it becomes somewhat modified in those with lungs. The intestine, which is long and well coiled in the young stages, is much shorter in relation to the body length of the adult. Forms leaving the water approach land conditions gradually, with developing limbs and changes in the circulation that throw more and more responsibility on the lungs, until finally the gills are absorbed, the clefts are closed, and the adult stage is reached. The thyroid and the hypophysis are very active, taking an important part in the changes from the infantile to the adult condition. By injecting the larvae with thyroxin, metamorphosis may be hurried, so that the change to the adult condition is made at a period long before it would occur ordinarily. *Ambystoma tigrinum* is well known for its axolotl stage, in which it may remain for a number of years or for life.

Résumé

Amphibians, the first tetrapods, appeared in the Devonian period. There are four subclasses, the extinct Stegocephalia, the Gymnophiona, the Urodela, and the Anura. They appear to have been derived from the lobe-finned crossopterygians, and they exhibit a variety of structures more or less modified from those of fishes. Their adjustment to the requirements of life on land is apparent in the division of the axial skeleton into regions, the strengthening of the connections between its parts, and the development of limbs, which replace the fins of fishes. The girdles of the limbs are organized to some extent to support the weight of the body. There is a striking reduction in the bones of the skull, particularly in those supporting and protecting the gills. The myotomic arrangement of the muscles is retained to a high degree, especially in the tailed forms. The early amphibians were covered with scales, but the modern amphibians are not. The skin is thin and consists of living cells, with many mucous glands, and there is a large cutaneous circulation. The digestive tract is rather simple. The tongue and oral glands are well developed in land forms. The lungs are thin-walled and are not extensively divided by septa; being unable to carry on all of the work of respiration, they are assisted by the cutaneous circulation. The heart is three-chambered, as a septum divides the atrium into two chambers, one for venous blood and the other for blood from the lungs. The aortic arches are reduced in number; the sixth is used as the pulmonary artery, and the fourth is specialized to form the systemic artery. The venous system is changed by a postcava replacing the post cardinals and by the union of the lateral abdominals, which now return blood to the heart through the liver. The nervous system is somewhat changed from fish conditions by the slight invasion of the roof of the telencephalon by nerve cells. The autonomic system becomes prominent. The nose is connected to the mouth posteriorly, and the glottis is somewhat improved by the addition of strengthening cartilages. The eye has better means of focusing, although the lens is still round as in fishes. A middle ear is added, derived from the fish spiracle; a stapes is formed from the hyomandibular bone of the fish; an opening, the tuba auditiva, connects the middle ear with the pharynx; and a tympanic membrane may be present. The organs of excretion are of the mesonephric type. An adrenal gland becomes prominent at the anterior end of the mesonephros. In males the Wolffian, or mesonephric duct carries both the spermatic fluid and the urine, but in females this duct carries only the urine, since the oviduct is a separate tube. Fertilization is usually external, although internal fertilization by means of spermatophores is common in tailed forms. A few amphibians are viviparous. All undergo metamorphosis.

CHAPTER XV

REPTILES

The reptiles are an important group because of their own wonderful variability and because of the fact that they supply the intermediate link between the birds on one hand and the mammals on the other. The first known reptiles appeared in the upper Carboniferous, or Pennsylvanian period, but it is probable that their actual separation from the amphibians came in the Devonian period. The earliest reptiles were much like the early stegocephalians, and from anatomical grounds it appears that they were closely related. *Seymouria*, one of the earliest cotylosaurs, had much in common with *Eryops*, one of the stegocephalians. The skull of *Seymouria* was of the heavy type with no openings except the foramen of the pineal eye; and the vertebral column was primitive, with ribs along the entire body except on the first cervicals and the last caudals. This series of ribs must have made the bending of the body rather difficult, although those of the thoracic region would be of great assistance in breathing. The girdles and limbs were also primitive, with rough joints and poor articulations. All these skeletal traits seem to have been inherited from stegocephalian ancestors.

The amphibians already had developed some structures necessary to fit them for land life, but further adaptations were made by the reptiles. Here again the first improvement came in respiration, which required an enlargement of the lungs and their higher development, so that the oxygenation of the blood could be carried on without the assistance of the gills or the skin. This was accomplished by making partitions in the lungs, so that the capillary surface was greatly increased. Further changes were made in the circulatory system, consisting of the enlargement of some vessels and the elimination of some of the connecting vessels formerly concerned with branchial respiration.

The skin, moist in the amphibians, was a source of danger, but in the reptiles it was entirely changed by the development of an outer layer of epidermis that was thickened and horny and had lost its mucous glands. In other words, the body was separated from the air by a layer of cornified epithelium that prevented evaporation. Generally the covering was made up of scales or plates of bone, although a few

reptiles on reverting to the water lost this covering and became smooth-skinned again, particularly the ichthyosaurs and the soft-shelled turtles.

The skeletal changes came slowly, since the earliest reptiles were not much better in this respect than the stegocephalians. The cotylosaurs and other early forms had many points in common with the stegocephalians, especially in the skeleton. Before the highest reptile stage was reached, the skull lost some of its superfluous elements and many changes were made in the parts concerned with locomotion. The vertebral column was further differentiated in all its parts. The ribs were reduced in the cervical and lumbar regions. The cervical region became more pliable by a refinement of its joints, and its first two vertebrae, the atlas and axis, became highly specialized to supply a more flexible joint with the skull. By a new articulation with the ribs, the sternum became much more serviceable and gave some assistance in forming a brace for the anterior girdle. The posterior girdle was also strengthened and its individual elements improved, so that they were better able to support the body. The limbs acquired better joints where movement was required, and the increasing specialization of muscles and nerves gave them better coordination. The toes were tipped with claws that were very useful in land life, especially for such purposes as climbing and digging, and served as a protection to the ends of the toes in walking.

Instead of two condyles, as in the amphibians, the reptiles have but one. As the reptile scale is ascended there is a progressive loss of the extra bones of the skull, either by elimination or by joining with other elements. The parasphenoid, striking as a landmark of the fishes and amphibians, becomes reduced or absent. There is a tendency toward the opening of the skull roof by the formation of arcades, so well shown in *Sphenodon* (Fig. 26).

There is a decided difference in the central nervous systems of the reptiles and the amphibians, and the reason may be looked for in the much higher plane on which the reptiles live. Land life adds much to the problem of existence, and there is a definite response in the nervous system, by increased size of the parts of the brain and spinal cord and by a multiplication of the number of fiber connections, thus making for better synchronism and coordination. The lateral line system is entirely lost, since it was a water adaptation, but the eye, nose, and ear are developed to meet the new conditions. Generally the required change is slight, but some radical modifications were necessary in the coordination of sight and hearing with the rest of the body. Equilibrium became more important, and its development called for a large increase in the nerve supply, so that the finer division and development

of the musculature could be useful to the animal. Instead of mass action of parts, there is a finer division of function and a more individual use of the different muscles, as in the toes and fingers. The earlier reptiles acquired extra nerve material to supply the huge development of the shoulder and hip regions by enlarged spinal cords, but obviously this was not the best plan, for a centralized nervous system could function much better. The brain consequently became enlarged in its relation to the body weight of later reptiles, with a decided increase in the size of the forebrain and a corresponding increase in the connections with the posterior part of the brain and the spinal cord.

The pallium, which was invaded by a small number of nerve cells in the amphibians, now has a large number of neurons. The cerebrum is large and swollen in comparison to that of the amphibians and has many more tracts between it and the rest of the brain. The corpus striatum is enlarged in size and in importance. The diencephalon becomes covered by the growth of the cerebrum and by the optic lobes, so that it does not show from the dorsal side of the brain at all. The cerebellum is variable, not strikingly large, and with flocculi in the higher forms. Two more cranial nerves, the eleventh and twelfth, are taken into the skull cavity and added to those already there. (Snakes still have but ten.)

The digestive system in reptiles is rather simple and not much advanced over conditions found in the amphibians. The stomach is long and spindle-shaped in the Lacertilia, as in *Ambystoma*; the duodenum is short, with the entering ducts of the liver and pancreas marking its distal limit. The pancreas is wedged in between the duodenum and the stomach. The intestine is not very long, and it ends abruptly in a large rectum, which in turn enters the cloaca. As in *Ambystoma*, there is a great difference in the diameter of the lower end of the intestine and the rectum. The stomach becomes more complicated in the higher reptiles, a gizzard being developed in many of them, since gizzard stones have been found in some fossil reptiles as well as in modern forms.

The lungs increase in size and diameter, and their internal structure is much modified by the building of a series of partitions extending the length of the lung, which greatly increase its capacity. The glottis is made more efficient by the addition of parts to improve its action. With further development of the larynx, the trachea becomes ringed with semicircular cartilages to prevent its collapse in breathing. The intake of the air is through the nostrils, or external nares, then into the pharynx through the internal nares. Instead of depending on the

mouth and throat for forcing the air into the lungs, assistance is now given by the ribs and intercostal muscles.

With the loss of the branchial circulation, the fifth aortic arch drops out entirely, the third functions as a part of the carotid, the fourth as the systemic, and the sixth as the pulmonary. The heart improves, and there is a partial division of its ventricle (complete in the Crocodilia and probably complete in the Pterodactyla). The arterial system remains much the same, but the venous system makes a number of changes, bringing it more to the right side of the body and removing it from the symmetrical plan of the sharks. New vessels appear and old ones are enlarged. The postcava, which was a new vessel in the amphibians, becomes the main passageway for the blood that formerly was led through the post cardinals. The renal portal system is being reduced and becomes of much less importance than in the amphibians.

The kidneys of reptiles are of the metanephric type found in birds and mammals. The nephrostomes have been lost, and there is no opening into the coelom. The ureter, a new vessel, conducts the urine from the kidneys; and the old mesonephric, or Wolffian duct is now used in the males for the transmission of spermatozoa and is vestigial in the females.

The reptiles introduce many changes in the details of reproduction. First, fertilization is always internal, and an intromittent organ, the penis, is developed for the introduction of the spermatozoa into the cloaca of the female. The egg is much larger than in amphibians, with more food supplied for growth and development of the embryo. In the oviparous forms there is either a leathery or chalky shell to protect the egg from drying and injury. All the rattlesnakes and gartersnakes, most of the horned toads, a number of lacertilians, and the extinct ichthyosaurs are known to bear living young. Two embryonic membranes, the amnion and the allantois, appear for the first time in the reptiles. Since they are also found in birds and mammals as well as reptiles, the name *Amniota* is sometimes applied to these three classes. The first membrane, or amnion, is a protective structure that surrounds the embryo, enclosing it in a fluid. The amnion is formed by the embryo from the material of its own body. The allantois, the second membrane, is also developed by the embryo and is used for respiration. In the placental mammals it becomes a very highly specialized structure for the transfer of food from the mother to the young and for the removal of waste. With these improved means of reproduction the reptiles have advanced far ahead of the amphibians.

Extinct Reptiles. — In the Mesozoic era the reptiles evolved into a bewildering assemblage of powerful creatures that dominated the world.

They became highly specialized and able to live in many different habitats, including water and air. The return to the sea was made by the mesosaurs, plesiosaurs, crocodiles, snakes, turtles, and other forms, the most perfect water reptiles being the ichthyosaurs. Large groups inhabited the fresh water of rivers, swamps, and lakes but did not become so specialized as those that went to sea. Those that remained on land varied greatly in size and agility, some being only a few inches long and others more than a hundred feet. One of the best-known divisions is the dinosaur group, composed of carnivorous and herbivorous forms of many species and genera, which spread all over the world. *Brontosaurus, Diplodocus, Trachodon,* and *Triceratops* (Fig. 23) attained great weight and bulk, since they lived at a time when food was abundant and easily obtained, and in a climate that was perfect for their best development. Changed climate and food conditions soon exterminated them. The carnivorous dinosaurs, magnificent in every respect, with specializations for preying on the more defenseless herbivorous types of the time, were bipedal, walking and jumping much as the kangaroo of today, and had small front limbs suited for handling food. *Tyrannosaurus* and *Allosaurus* (Fig. 23) were among the largest of the carnivorous forms.

Although possessing wonderful bodies, even the largest of the ancient reptiles had a comparatively small brain — thirty tons of muscle and bone controlled by a few pounds of nervous tissue. Some of the herbivorous forms, such as *Diplodocus* and *Stegosaurus*, developed a hip brain that was several times the weight of the head brain. Footprints of dinosaurs are very common in many parts of the world. The Connecticut River valley has large areas covered with hundreds of tracks. The finding of dinosaur eggs in the Gobi desert by Andrews was one of the most interesting discoveries of many years, for they were well preserved and gave some information of the home habits of the group.

The flying reptiles (Fig. 24), the pterosaurs or pterodactyls, were real fliers with bird-like air adaptations in their skeletal parts. The sternum and pectoral regions were adapted for the insertion of large flight muscles. The hand was modified for flying by the enormous elongation of the fifth digit, which supported the wing membrane. Light bones, thin and hollow-walled, completed their flying equipment. Again it seems probable that, with their activity, a four-chambered heart was present. They were very numerous and varied in size from a sparrow to those with a wingspread of thirty feet. Specimens have been found in Germany, with the web of the wing intact, so that its texture is known. Evidently they were smooth-skinned and without scales or plates.

Some of the extinct reptile stocks were probably ancestral to the

birds and mammals. The exact line of the bird ancestry is not known, but it appears to come through the Pseudosuchia, a reptile group related to the pterosaurs, crocodiles, and dinosaurs. The mammalian stem seems more certain, the Therapsida of Africa and other continents offering an ancestral type that is very satisfactory. The cynodonts of Africa, the best known, have a jaw with an enlarged dentary and a reduced articular region. The reduction of the quadrate seems to indicate the possibility of a new jaw articulation in which the squamosal would form the articulating element. Recent discoveries of Richard Broom seem to make this derivation of the mammals positive.

Modern Reptiles. — The reptiles of today comprise about 3500 species and are divided into five groups: the Rhynchocephalia, represented by *Sphenodon* of New Zealand; the Crocodilia, including the crocodiles and alligators; the Chelonia, or turtles; the Lacertilia, or lizards; and the Ophidia, or snakes.

Sphenodon (Fig. 26), is a small reptile, living in a very restricted area of the world. It is a left-over from a former group that was once more numerous. The Crocodilia are the largest reptiles living today, since some of the sea forms attain a length of forty feet. The land tortoises and sea turtles also attain weights of a thousand pounds, but generally the Chelonia are not very large. The lizards and the snakes are numerous everywhere and are the predominant types of living reptiles. The Lacertilia, though generally small, include a few large forms, such as the recently discovered Komodo lizard, of New Guinea, that reaches a length of thirteen feet. The monitors are about six feet in length. The Ophidia, or snakes, are very numerous, and some of the boas and pythons grow to a length of from twenty to thirty feet but such extremes are rare and the largest are usually not much over twenty feet. Poisonous forms of the reptiles are confined to the snakes, with the exception of the Gila monster (*Heloderma suspectum*), which is the only known poisonous lizard. This lizard has a poison as dangerous as that of the rattlesnakes, but fortunately for man, its means of injecting the poison is poor, through grooved teeth in the lower jaw. This transmission of the poison is not satisfactory but is very effective on small animals which the lizard is able to twist around and chew.

There are two groups of poisonous snakes in the United States, the Crotalidae and the Elapidae. The Crotalidae include the well-known rattlesnakes, water moccasin, and copperhead, known as the pit vipers. They are provided with hollow fangs and are able to inject their poison into the tissues. The poison is not protective but is used to deaden their animal food and is very effective since a rat will become quiet in a few minutes if the poison is well injected so that it reaches the blood

system. The paralyzed prey can then be swallowed with no danger to the snake. The crotaline poison attacks the blood system. The Elapidae have a single representative genus, the coral snake, of two species, found along the gulf coast and seldom more than four hundred miles from the coast. They are beautifully colored with cream, black, and scarlet and although small and harmless in appearance are very deadly. Their short, permanently erect fangs are capable of terrible execution if the opportunity offers. They are related to the cobra of India.

Sceloporus

Sceloporus, a genus of lizards found in practically all parts of the American continent, is used here to illustrate the reptiles. Its general appearance is typical of the group Lacertilia. The neck, when com-
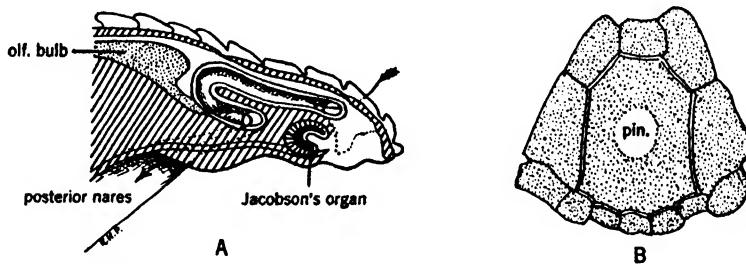
FIG. 293. A, sagittal section of the nose of Sceloporus. B, scales of the skull in the region of the pineal eye in Sceloporus.

pared with that of *Ambystoma*, is rather long and much more pliable, so that the head can be turned in any position — a condition very essential to land life. The legs also are longer than those of *Ambystoma* and are able to keep the body from the ground in either walking or running; but their position is still that of the emerging land animal, at right angles to the body, so that undue strain is placed upon them in locomotion. It is not until the birds and mammals are reached that the girdles and legs are pulled under the body to offer direct support. The body is covered with small epidermal scales, which serve for protection, offer little resistance in going through obstructions, and interfere in no way with free movement. The limbs are well formed, well muscled, and supplied with toes that are of real service in locomotion. Ten or more femoral glands are present on the posterior border of the femoral region. The eyes are protected with eyelids, the nostrils are well formed, and the eardrum is no longer on the surface but at the bottom of a shallow pit on the side of the head. The top of the head is

marked by the striking pineal eye (Fig. 293 *B*), which has offered so
much in the way of conjecture to the inquiring anatomist.

Skeleton. — The skull of *Sceloporus* (Fig. 294) differs in appearance
from that of *Ambystoma*, being not of the flat, platybasic, amphibian
type but of the tropibasic type characteristic of reptiles, in which there
is more depth and less width between the eyes, with some consolidation
and simplification of the parts of the skull (Fig. 295). The fish and
amphibian skulls differ radically, but the contrast between *Sceloporus*
and a modern amphibian is not nearly so striking. The paired condyles
of the amphibians are reduced to one in the reptiles. The brain case
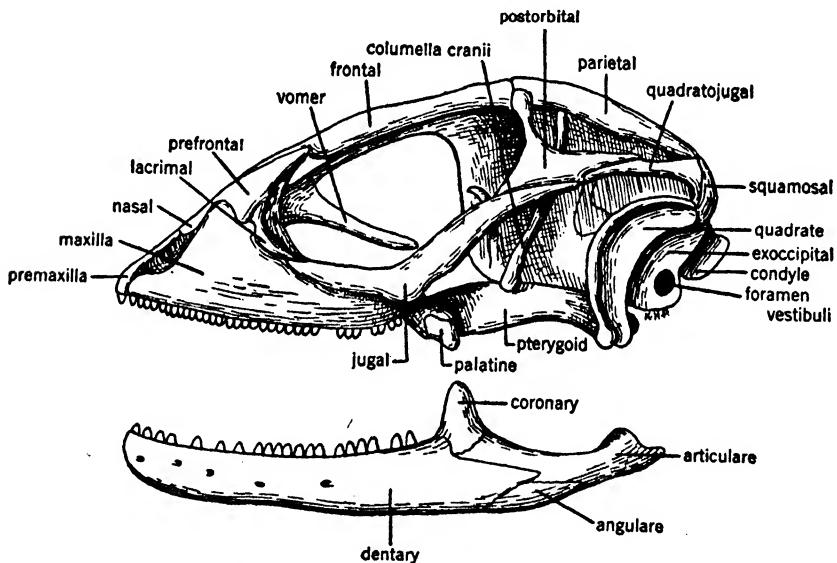
FIG. 294. Skull of Sceloporus, lateral aspect.

is enlarged and is better protected, although the anterior end remains
open. The four occipital bones are ossified, surrounding the foramen
magnum. The dorsal side of the skull has a fenestra, or arcade,
between the quadrate and the bones of the brain case. The skull is
narrow between the eyes, which are separated by a thin septum. The
quadrate is not fixed but slightly movable, and hence of the streptostylic
type as opposed to the monimostylic type in which the quadrate is
fixed. The squamosal ties the quadrate to the skull dorsally, and a
loose pterygoid connection on the ventral side supplies a brace in this
region. In the monimostylic Chelonia, the quadrate is fixed solidly at
all points. The ventral side of the skull shows a number of striking
differences, since the parasphenoid, the large covering plate of the

amphibian palate, is either lacking or but a vestige. The posterior choanae open far back in the mouth, much farther than in the amphibians. There is a large interpterygoid cavity, and the pterygo-palatine series is attached to the posterior end of the maxilla by a new element, the transpalatine, or ectopterygoid. The epipterygoid, or columella cranii, a bone peculiar to reptiles, is found in the lacertilians and in some other orders, forming a brace between the pterygoid and the parietal. (See Chapter IV.)
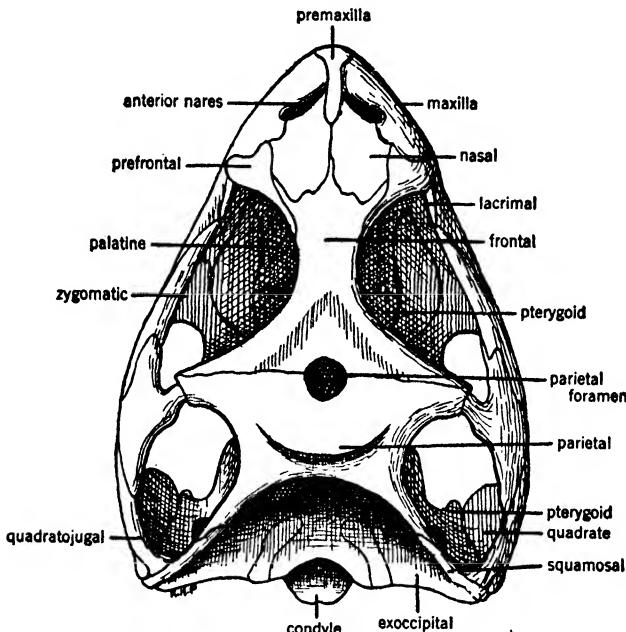
FIG. 295. Skull of Sceloporus, dorsal aspect.

Reptiles may nave teeth on the palatines, pterygoids, and other bones, but in *Sceloporus* they are found only on the dentary, premaxilla, and maxilla. The teeth in *Sceloporus* are pleurodont (Fig. 60), that is, firmly fixed to the sides of the jaw. The dentary has twenty-eight teeth, the premaxilla eight, and the maxilla about twenty-four. The teeth are long, open at the root end, and held to the inside of the jaw by connective tissue.

The mandible (Fig. 294) consists of seven bones: a dentary, coronary, articulare, angulare, surangulare, goniale, and splenial. Meckel's cartilage is reduced to a slight cartilaginous rod in a groove at the posterior end of the jaw and continuous with the articulare.

The visceral skeleton (Fig. 97) is typical of the lacertilians, con-

sisting of a number of parts of the old visceral structures of fishes. The anterior lingual process extends into the tongue, ending in cartilage. The median body is formed by the basihyoid, with two pairs of lateral elements, the anterior (hyoid) cornua and the posterior (branchial) cornua. The median basibranchials are shorter and cartilaginous. The visceral skeleton is well supplied with muscles and acts as a support for the glottis and the tongue.

The vertebral column is fairly well differentiated into five regions. The vertebrae are procoelous and are provided with pre- and post-zygapophyses. The cervicals, seven in number, consist of a ring-like atlas, an axis with a prominent odontoid process, and five cervicals supplied with ribs: The last two have much longer ribs, which are close to the sternum but not articulated with it. The thoracic vertebrae are not well differentiated from the lumbars, and all have ribs. Those of the thoracic region have longer ribs, and five are connected with the sternum by sternal ribs, three to the sternum proper and two to the xiphoid process. The ribs of the posterior end of the series become smaller as the sacrum is approached. The sacrals, two in number, are ankylosed together, forming a stable articulation for the ilium. The caudals are over forty in number, a part of them being supplied with

Y-shaped chevron bones which articulate with the ventral side. The caudal series is peculiar in the loose attachment of the vertebrae which permits a disarticulation in time of danger to the animal.

The cartilaginous sternum (Fig. 104) is well developed and is connected through three sternal ribs with the first three thoracic vertebrae. A large heart-shaped fontanelle forms a conspicuous opening in

Fig. 296. Right pelvic girdle of Sceloporus.

the cartilage. The large T-shaped interclavicle extends anteriorly along the medial line and supplies an articulation for the two clavicles, which in turn tie the shoulder girdle to this structure. The sides of the anterior region have grooves for the articulation with the coracoids.

The shoulder girdle (Fig. 104) consists of a cartilaginous suprascapula, an osseous scapula, and the coracoids. The coracoids, consisting of a procoracoid, coracoid, and epicoracoid, are not separated by sutures.

The pelvic girdle (Fig. 296) consists of three bones, the ilium, ischium, and pubis. The ilium is inclined posteriorly and articulated with the transverse processes of the sacral vertebrae. The pubis and ischium

are joined ventrally by the epipubic and hypoischial cartilages. All three of the pelvic elements take part in the formation of the acetabular cavity.

The anterior limb (Fig. 297, *A*) has the usual elements, the humerus forming the first segment. The humerus has a distinct head for articulation with the glenoid cavity of the scapula, and two tuberosities, one on each side. The distal end of the humerus has two condyles for the
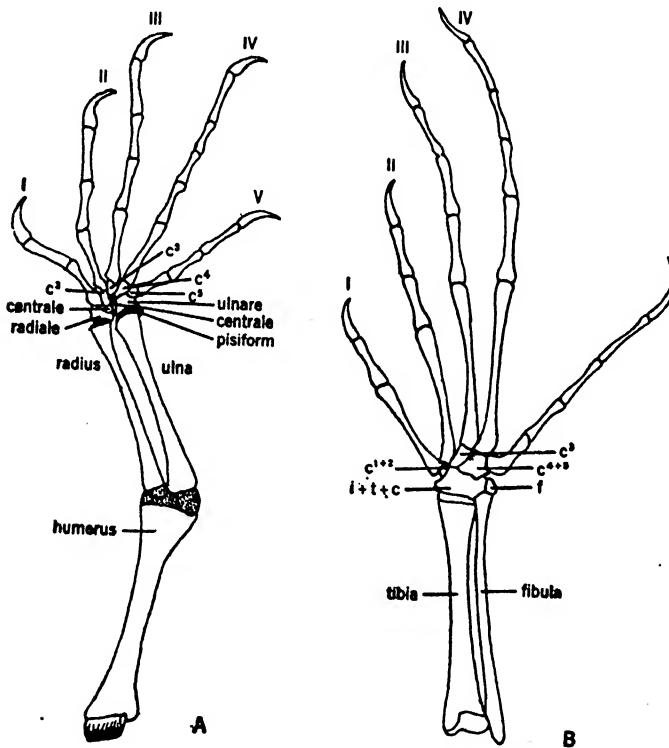
Fig. 297. A, right manus, B, right pes of Sceloporus.

articulation of the radius and ulna. The second segment, formed by the radius and ulna, is capable of some twisting. These elements are rather similar, with no great differentiation as found in higher forms. The proximal end of the ulna has a well-developed olecranon process and a facet for the articulation of the radius. Both these bones articulate with the carpus. The carpus is of the lacertilian type, the proximal row consisting of a radiale, two centralia, an ulnare, and a pisiform. The distal series consists of carpalia 2-3-4-5, with none for the first metacarpal. There is a tendency for an intracarpal joint between the

rows. The fingers are five in number and have the typical lacertilian formula, 2–3–4–5–4. All the fingers are tipped with claws.

In the posterior limb (Fig. 297, A) the first segment, formed by the femur, is rather long, an indication of well-developed locomotion. The femur has a rounded head for articulation with the acetabulum and a single trochanter on the mesial side. The condyles at the distal end supply the articulation for the tibia and fibula. A small patella is present. The second segment, formed by the tibia and fibula, shows some progressive changes, since the tibia is enlarged and the fibula reduced in importance, although retaining a place in the articulation with the tarsal joint. The tarsus is somewhat simplified by a consolidation of bones. The proximal row consists of a single element formed by the tibiale, intermedium, and centrale, with a small separate fibulare. A small element on the mesial side of the tibiale probably represents a centrale. The distal series consists of but two elements, the first being carpalia 2 and 3 and the second being carpalia 4 and 5. Typical of the lacertilians, the fifth metatarsal is a peculiar hook-shaped bone. The phalangeal formula is 2–3–4–5–4. (See Chapter IV.)

Digestive System (Fig. 298). — The mouth of *Sceloporus* is fairly large and has well-developed glands and a tongue that is free and protrusible. The Eustachian tubes connect the ears to the pharynx by large openings. The esophagus is short, and the stomach resembles that of *Ambystoma*, being rather straight and cylindrical in shape. The duodenum turns anteriorly for about half the length of the stomach, receiving the ducts from the liver and pancreas. The liver (Fig. 298) is large, of several lobes, and covers most of the ventral side of the stomach. The pancreas is elongated and placed in the U-shaped bend formed by the stomach and the duodenum. A small spleen is attached to the right side of the stomach. The intestine is short, since the food of this lizard consists mostly of insects. The rectum opens into the cloaca, which also receives the ducts from the kidneys and from the reproductive system. The lining of the coelomic cavity is made quite dark by a black pigment. (See Chapter VI.)

Respiration (Figs. 298, 300). — In *Sceloporus* the cutaneous circulation is lacking, and the lungs carry on all the work of respiration. The ribs, being movable and supplied with short muscles, are able to assist in breathing. The lungs are free in the body cavity, with no pleural sac. The glottis is a narrow slit, well protected by cartilaginous structures. The trachea, supplied with cartilages and located dorsal to the heart, sends a branch to each lung. The lungs are larger than in amphibians of the same size and have a somewhat different structure. Each lung is divided longitudinally by septa, which somewhat increase the total
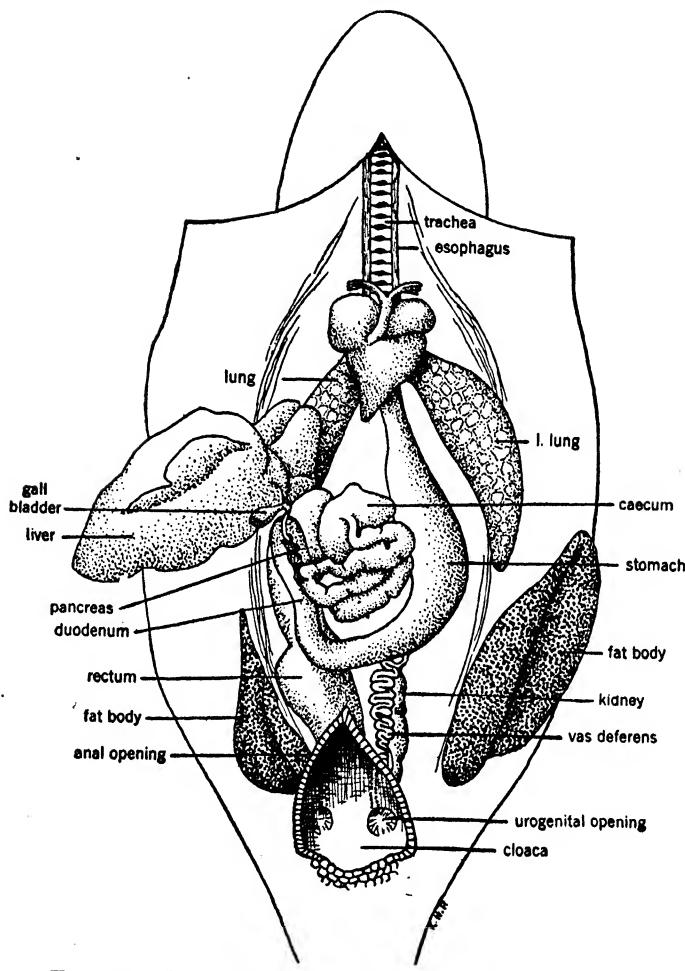
FIG. 298. Dissection of the visceral cavity of Sceloporus.
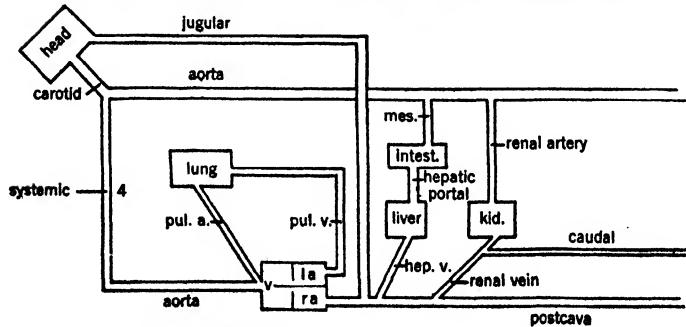
FIG. 299. Diagram of the circulation of a lizard.

lung capacity, and is provided with shallow alveoli. The right lung is about a third larger than the left. The bronchii do not divide into bronchioles, but each branch opens directly into the lung. The blood supply is from the sixth aortic arch, which is the pulmonary artery of all animals above the fishes.

Circulation. — The heart (Figs. 298, 301), as in all lizards, is three-chambered and has a pericardium. The atria are thin-walled and rounded; the ventricle is heavy-walled and pointed. The ventricle is partially divided by a septum, but the direction of blood to the proper outlet is effected by the same mechanical means as in the amphibians. The venous blood is so directed that it flows into the wide pulmonary arteries to the lungs, while the arterial blood, just returned from the lungs, is forced over the system.

Fig. 300. Lungs of Sceloporus.

The arterial system of *Sceloporus* (Figs. 299, 167), is fairly stable and quite similar to that of the amphibians except that the ductus arteriosus,
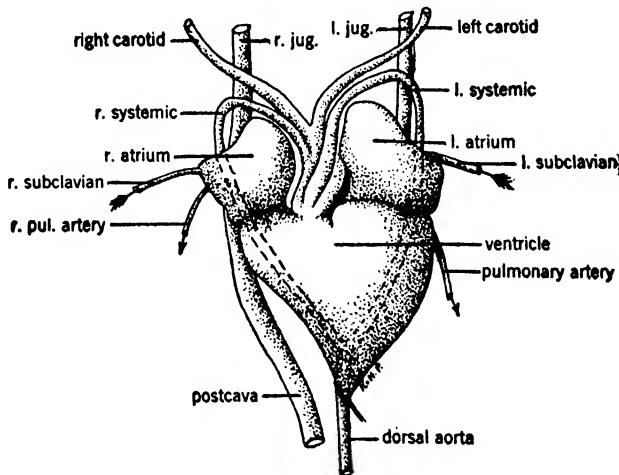
· Fig. 301. Anterior view of the heart of Sceloporus.

which joins the pulmonary to the fourth arch, is becoming vestigial. At the base of the aorta there is an extended splitting that is eventually to be continued to the heart, thus forming two separate vessels from the original single aorta. The right and left fourth arches join posteriorly

to the heart (Fig. 301) to form the dorsal aorta, from which branches are sent to the different parts of the body. The vessels to the head, the carotids, are formed from the third arches. Posteriorly the aorta lies against the dorsal wall of the coelom, extending back to the tail, where it is continued as the caudal artery.
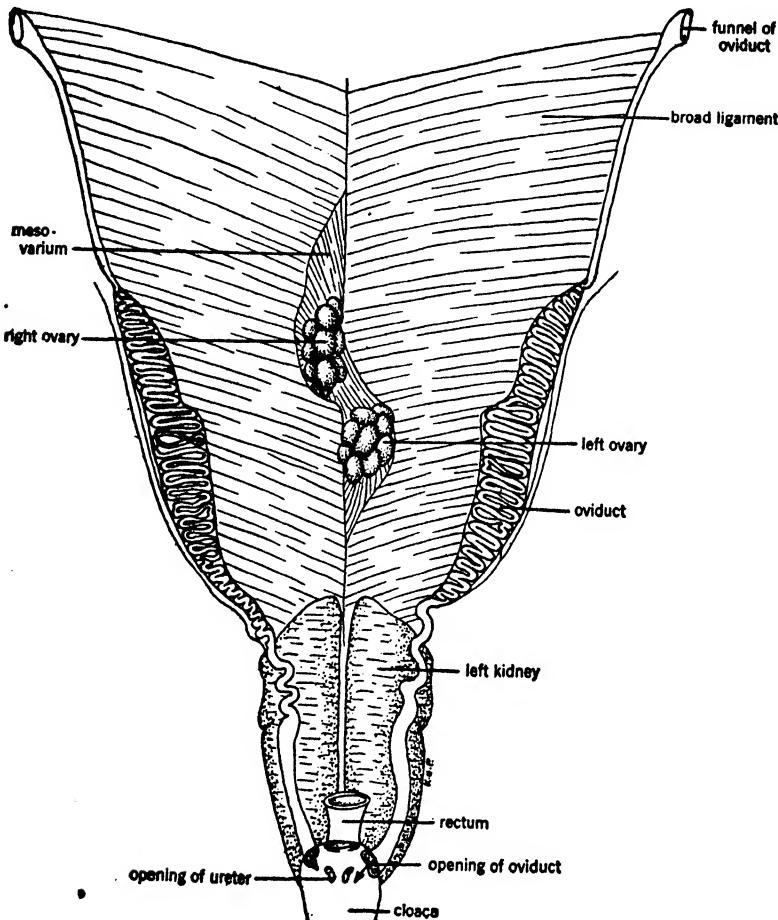
FIG. 302. Female urogenital system of Sceloporus.

The venous system (Fig. 173) shows a number of distinctive changes. The original symmetrical system of the shark is being pulled to the right side of the body and is losing its symmetry. The most distinctive change to be noted is the reduction of the renal portal system, coincident with the change in the type of the kidney, the loss of the post cardinals, and their change to azygos veins. The return of all the blood from the

posterior end of the body is through the postcava. The lateral abdominals continue to carry the blood from the limbs, emptying it into the postcava. The hepatic portal from the digestive tube remains unchanged throughout the vertebrates. (See Chapter VII.)

Urogenital System. — The type of kidney in *Sceloporus* is the metanephros (Figs. 302, 303) which is the highest type of kidney and that to be found in all reptiles, birds, and mammals. Compared to lower types of kidneys, it is more posterior in the body cavity, has a different origin, and is slightly different structurally, although the differences are not so much in the kidney itself as in its connections. The nephrostome, which opens into the coelom in both fishes and amphibians, is lost in reptiles. The renal portal system now tends to go through the kidney structure with no action by this organ. The ureter, the new outlet, which carries the urine to the cloaca, is entirely different in its origin and is in no way related to the mesonephric duct. There is now no connection between the reproductive system of the male and the metanephros, since the old mesonephric duct is now utilized entirely as a part of the vas deferens. The pair of kidneys extend along the dorsal wall of the body cavity and are covered by the pleuroperitoneal epithelium. Each ureter

FIG. 303. Male urogenital system of Sceloporus.

starts at the anterior end and extends posteriorly along the side of the vas deferens, and the pair of them enter the cloaca by a common duct. A bladder, generally found in the reptiles, is missing in *Sceloporus*. Two leaf-like yellow structures, the fat bodies, lie parallel to the kidneys.

In the male (Fig. 303), the testes are oval structures, secured to the body wall by a mesentery, the mesorchium. The right is much anterior

to the left and in contact with the right lobe of the liver.   The vas deferens is much convoluted anteriorly but becomes a simple tube posteriorly.   The convoluted portion was originally the mesonephric duct.   The penis consists of two small folds which, when not in use, fit into two pits posterior to the cloaca.

In the female (Fig. 302), the ovaries are about the size of the testes, but they are lobate and show the eggs through the wall, so that they have an entirely different appearance.   The right ovary is anterior to the left, with somewhat the relative position of the testes.   The oviducts empty into the cloaca by paired apertures just anterior to the entrance of the ureters.   The oviducts diverge from their outlet at the cloaca and extend anteriorly and laterally, each opening into a wide funnel.

Brain and Spinal Cord. — The brain of *Sceloporus* is typically reptilian (Figs. 304, 305) with changes in proportion of parts that easily separate it from that of the amphibians. There is a striking increase in the size of the telencephalon, which now becomes the largest region of the brain. Its anterior region is prolonged as a stalk, ending in an enlarged olfactory bulb from which the olfactory nerve is continued to the epithelium of the nose. The corpus striatum is enlarged, and the pallium shows a marked increase in thickness and in the number of neurons contained. Consistent with the increase in size of the pallium,
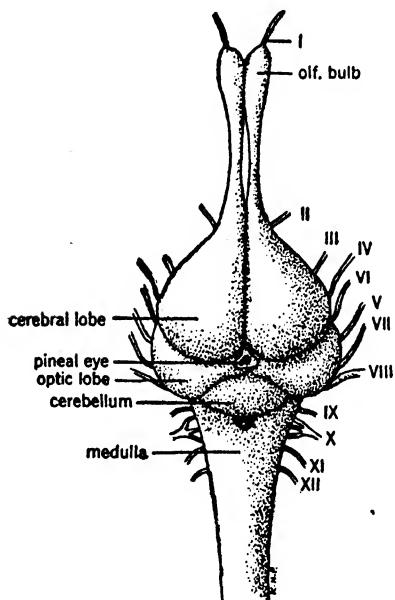
FIG. 304.   Dorsal aspect of the brain of Sceloporus.

there is an added number of connecting tracts now continued forward from the posterior parts of the brain to this region.   The diencephalon is covered by the telencephalon and optic lobes and is not evident from the dorsal side.   The third ventricle is reduced to a slit by the increased size of the thalami in its walls.   The dorsal wall has two outgrowths, the paraphysis and the pineal eye, the latter being well defined and extending to the pineal foramen of the skull.   (A cleared scale marks its position on the top of the head.)   The ventral side of the diencephalon is marked by the large hypophysis.   The mesencephalon has two large optic lobes, the corpora bigemina, which are forced laterally by the

posterior growth of the telencephalon. The metencephalon is well developed, although the cerebellum is not so large as in birds and no flocculi are developed. There is no unusual development of the myelencephalon, which has a choroid plexus and supplies the exits for the posterior cranial nerves. The brain has twelve cranial nerves since the eleventh and twelfth are now included in the brain case. The spinal cord continues the length of the body and has enlargements for the two pairs of limbs. (See Chapter IX.)
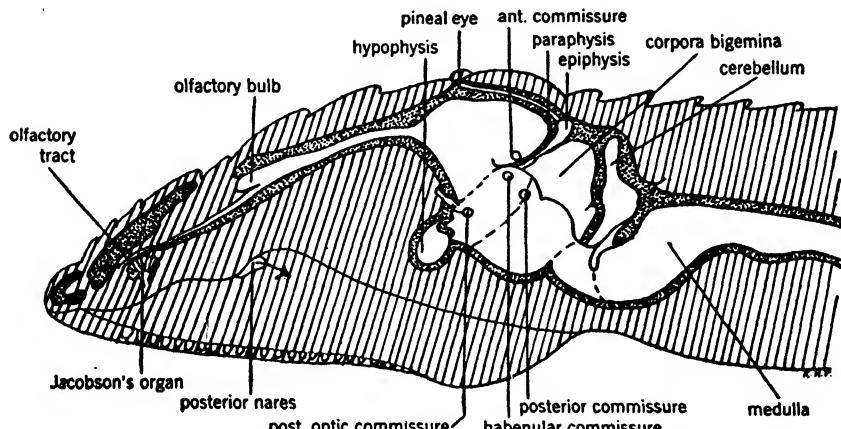
FIG. 305. Sagittal section of the head and brain in Sceloporus.

Sense Organs. — The nose of *Sceloporus* (Fig 293 *A*) is strictly a land type, the nostril opening into an S-shaped cavity, at the posterior end of which the olfactory nerve endings are spread over the surface. The nasal passage, although occupying but a short space because of its structural plan, is really quite long, and opens by the posterior nares to the roof of the mouth. The organ of Jacobson, which is relatively large and has a duct to the mouth, is probably concerned with the sense of smell. A nerve enters the papilla in the hollow cup at the anterior end of this organ.

The eye (Fig. 233) is provided with a third eyelid, the nictitating membrane, in addition to the usual pair of lids. Lacrimal and Harderian glands are present. The sight appears to be rather keen, and the power of focusing, by changing the shape of the lens, is greatly improved over amphibian conditions. The retina contains mostly cones, with very few rods. Twelve sclerotic bones surround the eyeball.

The ear (Fig. 223) is improved by a number of small adjustments that make it more adaptable to land conditions. There is an external auditory meatus, at the bottom of which the tympanic membrane is

placed. (In snakes, the external meatus is closed.) The 'lagena elongates and greatly increases in size, and the papilla basilaris appears in the lagena, foreshadowing the organ of Corti, which becomes the essential part of the hearing mechanism in higher vertebrates. There is a further development of the columella which consists of the stapedial plate, a columella auris, and an extracolumella, connecting the fenestra vestibuli with the tympanic membrane. The tuba auditiva, or Eustachian tube, is large and connects with the mouth through a wide opening. · Both the endolymphatic and the perilymphatic ducts have formed connections with the lymph spaces in the meninges of the brain. The external meatus is shallow and protected only by its surrounding walls. (In the crocodiles there are flaps that suggest the outer ear of the higher animals.)

Résumé

Reptiles made their appearance in the Pennsylvanian period, probably originating from the primitive stegocephalians. They are well adapted to conditions on land and have overcome the handicaps that still keep the amphibians from being independent of the water. The skin of reptiles is dry and usually is covered with scales or bony plates, except in those that have returned to the water. The lateral line is no longer present as in fishes. The skeleton is better organized, with decided improvement in all movable parts and better means of holding the vertebral column together. The axial skeleton is divided into five well-defined regions, the cervical, thoracic, lumbar, sacral, and caudal vertebrae being clearly differentiated. The girdles are arranged to form a better support for the limbs than in amphibians, and the limbs are in a ventral position, more advantageous for support of the body. The toes are equipped with claws. The thorax is strengthened by the addition of a sternum, to which ribs may be attached. The skull has a single condyle, in contrast to the double condyles of the amphibians. Some of the skull bones present in amphibians have been eliminated, and some new elements appear. The skull is tropibasic, in contrast to the platybasic skull of the amphibians. There is a reorganization of the skull bones, so that arcades appear in the skull roof. The visceral arches are reduced to the hyoid series. The digestive system is more highly specialized in all of its regions. The tongue and mouth glands are well developed. Respiration is carried on entirely by lungs in land forms. The lungs are subdivided by septa, which increase the functional area; they are not in pleural sacs, but hang in the body cavity. The glottis is improved by additional cartilages, and the trachea is ringed. The heart is three-chambered, as in amphibians, and there is also a partial division of the ventricle, so that the separation of venous and arterial blood is better than in the amphibians. The aortic arches are still more modified by the splitting off of the sixth to become the pulmonary arteries and the fourth to become the systemic vessels. The changes in the venous system consist in the reduction of the post

cardinals to form the azygous veins, the development of the circulation in the postcava so that it returns most of the blood from the body, and the decrease in the amount of blood carried by the renal portal system. The kidneys are of the metanephric type and have new ducts, the ureters, which conduct the urine to the bladder or the cloaca. The nephrostomes are lost. The vas deferens is the outlet for the testes. Fertilization is internal, and a penis is developed in some reptiles. Some reptiles are oviparous, and others viviparous. The oviducts are still more specialized for the formation of eggs that are to be laid on land. Two new membranes, the amnion and allantois, envelope the embryo. The brain is noticeably larger than in the amphibians, in proportion to the size of the body, and its connecting tracts are more numerous. The pallium, or roof of the telencephalon, becomes further invaded by nerve cells, suggesting the condition of this structure in mammals. The telencephalon is larger than in the amphibians, and there is a better development of the cerebellum, with additional structures, the lateral flocculi. The spinal cord becomes enlarged in the regions that supply the limbs; in some ancient reptiles the pelvic enlargement of the spinal cord was greater than the brain. The nasal cavity is improved and has a more extensive olfactory area, the internal nares being pushed posteriorly, and a Jacobson's organ is prominent. The eyes have still better means of focusing, the lids are improved, and there is a specialization of the glands to keep the eyes moist. The ear usually has an external meatus, and the tympanum is internal. The stapes is connected to the drum through a columella and an extra-stapedial cartilage.

CHAPTER XVI

BIRDS

The ancestry of birds leads back to the reptiles of the Mesozoic, where some light-boned, large-brained, active group of the Pseudo-suchia, related to the dinosaurs, pterodactyls, and crocodiles, developed a flying wing of the avian type. There are varying opinions as to whether the actual bird stem came up through an arboreal or a cursorial pre-bird ancestry, with the greatest weight of the argument for the arboreal, since it seems probable that an animal could get into the air by means of tree life more easily than by volplaning from the ground. In arboreal life, the fore limbs would be used at first for grasping, but by becoming webbed would give enough support for short sails through the air, and eventually lead to flight. By the development of feathers these intermediate forms were enabled to maintain a more stable temperature and to be more active. Early, there was a splitting into two branches, the running and the flying. Some writers have insisted that these two groups came from two origins instead of one, but this assumption seems rather unnecessary, and there is little evidence to support it. From what is known of the earliest birds, the Saururae, it is possible to have a wing serviceable for flight, and at the same time equally good for grasping limbs.

The first known birds appeared in the Jurassic, and their remains have been found at Solenhofen, Germany. Two fairly complete specimens are known, *Archaeopteryx* (Fig. 27) at London and *Archaeornis* at Berlin. Some other fragments have been found, but these represent the only complete specimens. They were small, about the size of a crow, and covered with feathers in true bird fashion, but their anatomical features are about as close to the reptiles as to the modern birds. Naturally, they inherited a number of reptilian traits. Without the imprints of the feathers, these fossils would probably be placed in the doubtful class today. The Saururae, to which these two belong, differed from modern birds by having conical teeth, free fingers on the wing, no uncinate processes, neck ribs long and free, fingers with claws, tail long and composed of many vertebrae, each vertebra with a pair of feathers, sternum small, ribs needle-like and weak. The brain was small and reptile-like. Anatomically the skull is easily differentiated from modern birds but not so easily from the reptiles. The vertebrae were amphicoelous as in some of the later birds. These primitive birds

could lead a very active life and escape some of the physiological and anatomical problems besetting the reptiles (Fig. 27).

The next group of birds is represented by quite a number of specimens found in the Cretaceous of Kansas. One of these, a diver, *Hesperornis regalis* (Fig. 28), was about four feet long with vestigial wings, a fine set of needle-like teeth, and amphicoelous vertebrae. A second water-bird, *Ichthyornis impar*, found a little later geologically, was also toothed, gull-like in appearance, and of medium size. It is highly probable that at this time birds were widely differentiated and generally distributed, but little is known of them since bird remains are so likely to be destroyed.

The birds of the Tertiary were much like the birds of today, with about as many orders. From discoveries made in the asphaltum pits at Rancho de la Brea and in other places, the birds of this period are better known. The carinates and ratites existed in the Eocene. *Diatryma*, a typical ratite form, was found in the United States, and in South America and in other parts of the world these walking birds must have been rather common. *Phororhacos*, frequently shown in books of bird history, was a hawk-like form with a head as large as that of a horse. It must have been a wrecker of the small mammalian fauna of the locality. *Aepyornis*, a wingless moa from Madagascar, was seventeen feet in height and laid an egg thirteen inches long and nine inches in diameter. The moa population of New Zealand was very extensive, consisting of both large and small forms. The largest, *Dinornis maximus*, was about ten feet in height. The *Kiwi* (Fig. 29), a modern representative, is about the size of a chicken. Today the walking birds are very limited in their distribution, being found in South America (rhea), Africa (ostrich), South Western Asia (ostrich), and Australia and New Zealand (emu, cassowary, *Apteryx*). These are the last representatives, and they seem doomed to extinction with the gradual encroachments of civilization (Fig. 29).

The carinates are very numerous, both in species and in individuals, and seem able to hold their own against most of the handicaps that man has placed upon them. They are very highly specialized and are able to live under most conditions, from the ice regions of the poles to the tropics. Some flightless forms have appeared, such as the penguin and the great auk.

GENERAL CHARACTERISTICS OF BIRDS

Birds have developed some stable characters found in no other group. For example, no other class has a covering that resembles feathers. These develop much as do the scales, but the final product is entirely

different and perfectly distinctive. Scales are retained on the feet and legs of most birds. No member of the class has lost this coating, although parts of the feather may be lost, resulting in the hair-like covering of some of the flightless birds. The penguins, reverting to a water life, have scale-like feathers covering the wings. The single condyle of the skull is shared with the reptiles. The brain is much larger than that of any reptile. The temperature regulation is good, but the temperature is not absolutely stable. A bird with a temperature of 112 degrees may live comfortably in a temperature of −30 degrees, because of the fine insulation, physiological activity, and the efficiency of the heat-regulating devices. They are bipedal animals with the anterior limbs modified for flight, a character shared with both the reptiles and mammals. The mandible and maxilla are sheathed in a horny covering forming the bill. The bones of the flying forms are light, pneumatic, and often connected with the lungs by ducts from the airsacs. The right ovary and its duct atrophies, leaving only a vestige. No modern forms have teeth. One anatomical peculiarity, the retention of the right aortic arch, differentiates birds from all other classes. The wings have retained but three digits in modern forms, and the feet have but four toes. There is a general similarity between the reptiles and birds, which extends to every part of their anatomy.

Every part of the bird skeleton is specialized for flight, with much fusion of bone to secure rigidness, strength, and stability.

The skull is fused into one piece in the adult. The only movable parts are the quadrate and mandible, except in parrots and a few others in which the maxilla is movable. The skull is very light, even in large-headed birds such as the toucans and pelicans. The long slender jugal and quadrato-jugal, and the large brain case, serve to separate birds from reptiles. The brain is covered anteriorly by the ossification of the lateral sphenoids. The elongated anterior part of the skull is formed by the prolongation of the facial elements, thus forming the beak. The pineal foramen has disappeared, the eye sockets are large, and the palate is open as opposed to the solid structure of most reptiles.

The vertebral column is specialized for flight, with the elements fixed in a rigid manner, so that the mechanics of flying are not interfered with by loose parts. The neck vertebrae are numerous and quite pliable, with small ribs joined to the vertebrae. All modern birds have vertebrae with saddle-shaped ends of the centra. The vertebrae in the thoracic region are joined together by ossified tendons. The lumbars, sacrals, and a part of the caudals are ankylosed together to form a synsacrum, which is covered by the greatly enlarged ilium. The type of the pelvis is the same as that found in bipedal reptiles. The

ribs are rather stocky and fastened together by uncinate processes. A well-developed series of sternal ribs attach the ribs to the sternum, thus forming a solid basis for the insertion of flight muscles. The shoulder girdle forms a triangle, with the humerus articulating at the apex. The coracoids act as a brace for the sternum. The carinate sternum is made distinctive by a large keel to which the pectoral muscles are attached. The vertebrae and the ribs, thus connected with the sternum, form a complete bony ring that is comparatively rigid. The anterior limbs are modified for flight by consolidation and reduction of parts in the carpus and manus.

The posterior limbs have a number of characters in common with the bipedal dinosaurs. The tibia and fibula are fused to form one element, to which the proximal series of tarsal bones are joined, to form the tibiotarsus; the distal series of tarsals join the fused metatarsals to form the tarsometatarsus. The three metatarsals are fused into one bone with three articulations on the distal end for the three toes. The first digit has been lost, the remaining toes being 2, 3, 4, 5. The toe formula resembles that of the reptiles.

Gallus

The common chicken, *Gallus domesticus*, is used to illustrate the anatomical parts of birds. The chicken belongs to the carinate birds, and to the order Gallinae, in which are the chickens, turkeys, grouse, pheasants, and quail. The chicken is close to the pheasant in its structure and relationships, and its origin can probably be traced to the jungle fowl of Asia with an intermixture of Aseel and probably other stocks.

Feathers. — The covering of feathers is typical of birds, and, although the chickens are not good fliers, they have all the parts that fliers should have. The flight feathers are in place on the wings, and the tail is functional as a rudder. The skin pattern of a picked fowl shows the feathered areas (pterylae) and the featherless areas (apteria). Feathers vary from the perfect specimen, in which all the typical parts are present, to the hair-like feather in which only the shaft is left. The perfect feather (Fig. 55), such as the flight feathers, consists of a shaft, with two parts, a base, or hollow quill, and the rhachis, to which the vane is attached. The vane consists of a series of barbs, extending out from the rhachis, which, in turn, have a series of small processes, the barbules. Barbicels, or hooklets, fasten the barbules and barbs together, so that a disarranged feather is easily repaired. The inferior umbilicus opens at the base of the quill, and the superior umbilicus at the base of the

vane. The feathers covering the body are similar in structure to flight feathers. When the hooklets are absent the feathers are downy in character (Fig. 54), as in the down of geese, ducks, and young birds generally. The presence of many of these plumulae gives the birds a fluffy appearance, in contrast to the smooth-feathered adult. A third type, the hair feather of filiplume, consisting only of the shaft, is found around the eyes and under the other feathers.

The skin is thin, consisting of two layers, the epidermis and the dermis. The skin is not glandular, the only large gland being the one found at the root of the tail and used for giving an oily coat to the feathers. (See Chapter III.)

Skull. — The separate bones of the skull (Fig. 306) fuse early, and most of the sutures are obliterated in the adult. The brain case, which is particularly well knit together, is formed by the fusing of the frontals,
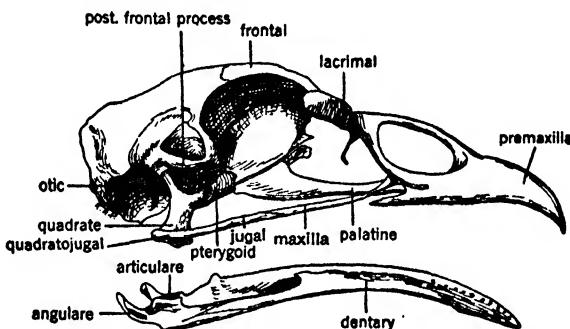
FIG. 306. Skull of Gallus, lateral.

parietals, four occipitals, orbito- and alisphenoid, squamosal, basisphenoid, the bones of the otic capsule, and a vestigial parasphenoid. Three series of bones extend forward from the brain base: (1) the nasal, ethmoid, and premaxilla constitute a dorsal series extending forward from the frontal; (2) the quadrato-jugal, jugal, and maxilla form a lateral series extending from the quadrate to the premaxilla; (3) a ventral median series, consisting of the pterygoid and palatine, connect the quadrate with the premaxilla. The chicken has a large bony septum, the interorbital, which may be called the median ethmoid. Because of the loose quadrate, some movement is possible in the maxilla and premaxilla. A conspicuous lacrimal with a long ventral spine is in the usual position in the anterior corner of the eye socket. The orbits are comparatively large. The mandible is quite reptilian in its character, usually consisting of a dentary, angulare, articulare, coronoid, and dorsal coronoid. (See Fig. 306.)

Visceral Skeleton. — The visceral skeleton (Fig. 317), which is small, consists of an anterior element, the paraglossal; two anterior cornua; a median entoglossal, or basihyal; a posterior basibranchial, or urohyal; and two posterior cornua, each consisting of ceratobranchial 1 and epibranchial 2.

Vertebral Column. — The cervical vertebrae, of *Gallus* are sixteen in number, forming a long flexible neck. The atlas, the first cervical, is ring-like and provided with a facet for the condyle of the skull. The axis, the second cervical, is small, ribless, and provided with an odontoid process for the articulation with the atlas. The remaining cervicals have small, fixed ribs, except the last three, which are free. The centrum is long in the typical cervical, with a peculiar saddle-shaped articular surface at the posterior end. The neural spines are present on only a part of the cervicals.

The thoracic vertebrae, five in number, become a part of the rigid region developed in the bird body. The first three fuse with the last cervical, making a solid section, with joined neural spines and hypapophyses. The fourth thoracic is free, and the fifth, or last, joins the lumbars to assist in forming the synsacrum. The lumbars, sacrals, and a part of the caudals are fused together, making a solid articulation for the ilium. It is difficult to differentiate these regions, but it is probable that the sacrals number two as in the reptiles. The lines of demarcation are clear between the individual vertebrae, although their centra are joined and fused. The free caudals, four or five in number, with a fused series, the pygostyle, terminate the tail. This region is very important in flying birds, since it carries the tail feathers and is valuable in steering. (See Chapter IV.)

Ribs and Sternum (Fig. 106). — Five bicipital ribs attach the thoracic vertebrae to the sternum. Intervening between them and the sternum are the five sternal ribs which fit into facets on its side. Each of the first four is provided with an uncinate process, a small flap of bone that overlaps the following rib.

The sternum (Fig. 106) is a large bone, covering the ventral side of the body and projecting posteriorly so as to protect the whole abdominal wall. It is convex on its ventral surface and somewhat narrowed at the posterior end, with a xiphoid process along each side. The median line is drawn out into a keel, which is used for the attachment of the flight muscles. The glenoid cavity is formed at the junction of the scapula and the coracoid.

Appendicular Skeleton (Fig. 106). — The shoulder girdle consists of three bones, the scapula, coracoid, and clavicle. The scapula is sickle-shaped and lies along the side of the thoracic vertebrae. The coracoid

is heavy, taking much of the stress of flying.   Its proximal end articulates with the scapula, and its distal end is joined to the sternum by an elongated articulation, fitting into a facet.   The clavicles (furcula, or wishbone) are joined at their distal ends, and articulate with the coracoids at their proximal ends.   The girdle, though light, is very strong, because of its rigid bracing.

Anterior limb (Fig. 120). — The anterior limb is modified for flight, by numerous changes in the carpus and hand.   The humerus is of the usual bird form, the radius and the ulna slightly specialized, the ulna having the flight feathers attached to its posterior border.   The bones of the carpus are more specialized, the radiale and the ulnare remaining free, while the distal row of carpals joins with the metacarpals to form the carpometacarpus.   These metacarpals are considered as parts of the second, third, and fourth digits.   Digit 2 has a short metacarpal and one phalanx, digit 3 a large metacarpal and two phalanges, and digit 4 one long metacarpal and one phalanx.   In birds generally, there is much variation in the manus, since it is so closely correlated with the type of flight and the rapidity of the movement of the wings.

FIG. 307.   The foot of Gallus.

Pelvic Girdle (Fig. 102 *D, F*).— Since birds are bipedal, the pelvic girdle is specialized for this form of locomotion.   There is a close similarity of the girdles of the birds and dinosaurs, since both have the elongated ilia.   In *Gallus* the ilium is greatly elongated and joins with the synsacrum, thus giving an extremely long and strong articulation. The ischium extends backward, its posterior end free as is the pubis. The pubis is a long, slender bone that extends posteriorly, parallel to the ischium.   A small prepubic process is present, just anterior to the acetabulum.

Posterior Limb (Figs. 307, 308). — The posterior limb is marked by a fusion of the tarsals and metatarsals. The femur, with a prominent articular head, is bird-like but not strikingly modified. A patella is present. The tibia and fibula are joined, and to this combination is added the proximal row of tarsal bones, forming the tibiotarsus. The fibula, though fused with the tibia at the proximal end, is free at the distal end and does not reach the tarsus. Three tarsal elements are joined to the metatarsals to form a single bone, the tarsometatarsus,

with three heads at the distal end for the articulation of the toes. No trace of the joining of the metatarsals remains in the adult, but in the embryo the origin is plain. There is some question as to which toe is lost, the fifth or the first. The phalangeal formula of the toe bones is 2, 3, 4, 5. The posterior, or second, digit has a small, partially developed metatarsal, which is attached to the others by a tendon.

Digestive Tube. — The digestive system (Fig. 309) in *Gallus* is typical of the grain-eating birds, with some modifications for special treatment of hard food. The mouth cavity is typical, the tongue being pointed, fairly long, and capable of movements

FIG. 308. A, tibiotarsus, B, femur of Gallus.

necessary to handle food properly. The posterior nares enter the roof of the mouth by a narrow slit. The posterior end of the palate has a cross ridge of horny papillae, and the base of the tongue is supplied with a series of the same structures. The Eustachian tubes ·enter the anterior part of the pharynx by a common aperture. The glottis is a narrow slit at the base of the tongue protected by cartilages. The mouth is well supplied with glands, having three submaxillary glands posterior to the premaxilla, a sublingual at the base of the tongue, palatals in the roof of the mouth, and a gland at

the angle of the mouth that is probably a parotid. The esophagus is made up of the same layers as the rest of the tube except that it lacks the serosa. The crop, a dilated region of the esophagus, serves as a storage place in which hard food is softened. The stomach is made up of two parts, the proventriculus and the gizzard. The former, which is not much larger in diameter than the esophagus, is supplied with the glands usually found in the anterior part of the stomach, which pour their secretion over the food material and soften it. The gizzard, rounded and somewhat flat, with glands at the anterior and posterior ends, is highly muscular, with heavy walls and a horn-like lining. The horny pads, together with stones always found in this organ, form a grinding mill, capable of reducing hard grains to a paste. The exit of the food, through the pylorus, is close to the entering tube. The rather long duodenal loop surrounds the pancreas, the liver being at the distal end. The entrances of the ducts from the liver and pancreas mark the distal end of the duodenum.

The intestine is about sixty inches long, with little differentiation; the folds are held together by the mesenteries. In cross-section, the inner layers show deep
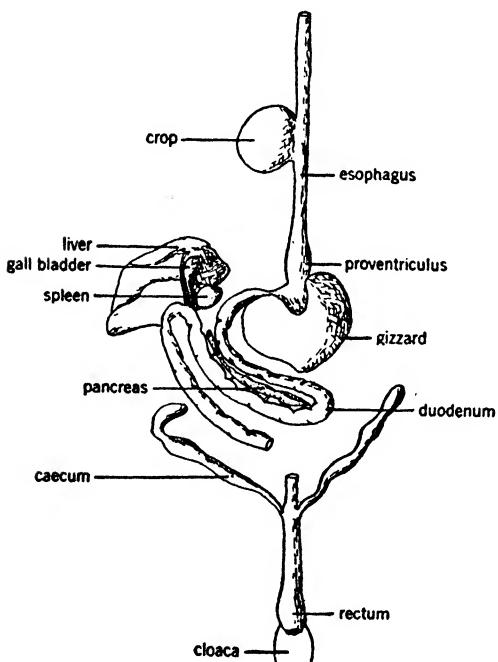
Fig. 309. Digestive system of Gallus.

folds, thus giving a large increase in the area of the absorptive surface. Below the esophagus, all the digestive tube is covered by the serosa. The beginning of the rectum is marked by two caeca, about seven inches in length. The rectum, with a length of three inches, opens into the cloaca. The cloaca is divided into two parts: the anterior, into which the rectum enters; and the posterior, into which the kidneys and the reproductive organs have their outlets. A small gland, the bursa of Fabricius, of problematic function, is located on the dorsal portion of the cloaca.

The liver (Fig. 309) has two lobes, a right and a left, with a large gall

bladder, and the two ducts enter the duodenum at its distal end. The pancreas fills the space between the folds of the duodenum, its ducts entering close to those of the liver.

Respiration. — The air enters the nostrils and is taken into the lungs through the glottis by movements of the skeleton, so that there is an easy passage through the lungs (Fig. 310) at all times. The glottis has a good skeletal arrangement of four cricoid and two arytenoid cartilages. The trachea is incompletely ringed with cartilage, with the sound-producing organ, the syrinx, at the posterior end. The syrinx consists of an enlarged chamber, formed of cartilage, with a median bar support-
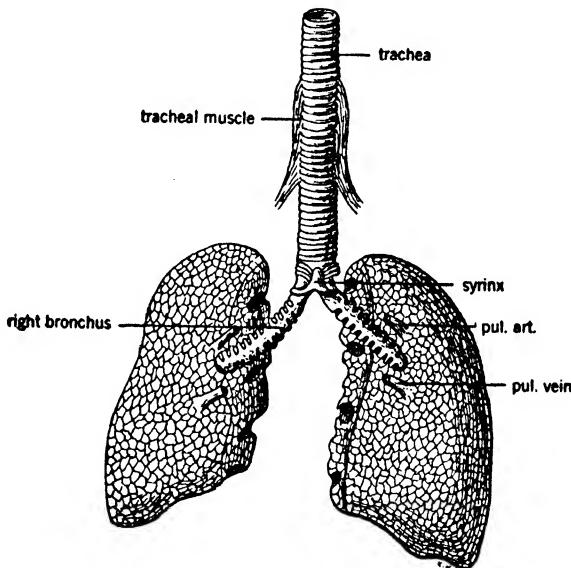
Fig. 310. Lungs and trachea of Gallus (airsacs omitted).

ing a semilunar membrane whose vibrations produce the sound. The structure is well muscled and is highly specialized in song birds. The trachea divides into two bronchii leading to the lungs themselves. The lungs, spongy and much higher in development than those of the reptiles, lie along the back, close to the ribs, protected by a fold of the peritoneum. The peculiarity of the bird's respiratory system lies in the development of large accessory airsacs that extend to different parts of the body, thus making it pneumatic.

The accessory airsacs consist of six pairs: a cervical pair at the base of the neck; a clavicular pair in the region of the clavicle; three pairs connected with the abdominal cavity, anterior, intermediate, and posterior; and a small pair in the axilla. These are connected with

the bronchii so that they get a direct supply of air, and the lungs have all the respired air taken out at every breath. It is probable that these sacs have an important function in keeping up the high tempera-

ture as well as assisting in respiration. The sacs themselves are not concerned in the aeration of the blood, since they have no capillaries, but act indirectly in the exchange of air in the lungs. (See Chapter VIII.)

Circulation.—The heart of *Gallus* (Fig. 311 *A, B, C*) is of the typical bird form, large, and with four chambers. The sinus venosus has been added to the wall of the right atrium. The arterial and venous bloods are completely separated, and there is no opportunity for the bloods to mix as in the reptiles. The jugulars join to form the anterior cava, and the post-cava returns the blood from the posterior end of the body, delivering it to the right atrium, which in turn sends it to the right ventricle through the flap-like atrio-ventricular valve. This valve is not like the tricuspid of the mammals. There is a slight development of the chordae tendinae, which assist in holding this valve. The

Fig. 311. Heart of Gallus: A, ventral; B, dorsal; C, cross-section of ventricles.

complete separation of the aortae permits the blood to go through the sixth aortic arch, now the pulmonary, to the lungs. The right ventricle is small, crescentic in shape, and partially encircles the left

ventricle. Semilunar valves prevent the return of the blood from the pulmonary artery. The return of the blood is through the pulmonary veins, one from each lung, entering the left atrium through a united vessel. The left atrio-ventricular valve is formed by two flaps of tissue attached to the walls of the ventricle by chordae tendinae of the avian type. It is very serviceable but not so heavy as the bicuspid valve of the mammals. The left ventricle (Fig. 311 *C*) is much heavier than the right since it must send the blood over the whole body.

Arterial System. — The fourth aortic arch (Fig. 160) on the right side forms the systemic aorta; the one on the left side is entirely obliterated. Large and heavy at its origin, it sends off a pair of large innominates, which divide into the subclavians, to supply the heavy pectoral muscles, and the carotids, to supply the head. The aorta descends at the anterior end of the heart, giving off branches in the manner typical of the higher animals (Fig. 174).

Venous System. — The venous system in birds (Fig. 168) is much like that of reptiles, but the manner of entering the heart is simplified, the duct of Cuvier and the sinus venosus being taken into the heart walls. Blood from the head and anterior parts of the body comes to the right atrium through the precavas, which in turn are formed from the joined jugulars and subclavians of each side. The blood from the posterior part of the body is conducted to the right atrium through the postcava. The blood from the intestines and the digestive system goes to the liver through the hepatic portal system and is returned through the postcava. The renal portal system is disappearing as such, although the large veins from the posterior end of the body still go through the substance of the kidney. The lateral abdominals have disappeared but are probably represented by the epigastric.

Ductless Glands. — Birds have several developed ductless glands now known to be so important. In *Gallus* the thyroid, parathyroid, pineal, hypophysis, adrenals, and gonads all serve their function in different ways. The thyroid is an ovoid structure about thirteen millimeters long with a width of seven millimeters, located low on the neck at a point where the common carotid and jugular cross. The parathyroids are a small pair of bodies attached to the posterior end of the thyroids. The thymus becomes vestigial in the adult. The adrenal, a yellowish body, is on the mesial side of the anterior lobe of the kidney. The hypophysis and pineal are attached to the brain.

Excretion. — The kidneys (Figs. 312, 313) are three-lobed structures closely applied to the synsacrum, having a length of about sixty-five millimeters. The ureter originates on the anterior lobe, extends posteriorly along the ventral side, and enters the dorsal side of the cloaca. The adrenals are attached to the mesial side of the anterior lobes.

Male Reproductive Organs. — The testes (Fig. 312), posterior to the lungs and anterior to the kidneys, vary in size according to age, being about fifty millimeters long in a mature cock. The vas deferens is a convoluted tubule that extends posteriorly along the ventral surface of the kidney, paralleling the ureter for a part of the distance, and enlarging slightly at the distal end to form a small seminal vesicle, which enters the urogenital region of the cloaca by a papilla. The papilla, when enlarged as in the duck and ostrich, though not in the chicken, serves as a penis.

Female Reproductive Organs (Fig. 313). — The single left ovary is posterior to the lungs, and in a mature hen it resembles a bunch of grapes, with eggs in all stages, from small ova to those ripe and ready to be erupted. The oviduct is quite extensive in a laying hen, being about thirty-five centimeters in length, and is divided into four regions. The first region is the funnel, or ostium tubae, which is wide and of ample size; fertilization occurs in the proximal end of this region. The second region is heavy-walled, and lined with albuminous glands. The third region adds the membrane, and the fourth supplies the egg with its calcareous shell. A short vagina opens into the cloaca, through which the egg is laid. The right oviduct is short and abortive, remaining only as a vestige, with an opening into the right side of the cloaca. (See Chapter XI.)

Brain. — The brain of *Gallus* (Figs. 206, 207) is larger in proportion than that of the reptiles, being short and wide, with a greater development of the anterior lobes than in any of the lower vertebrates, and with more evident flexures. Since birds must meet new conditions not encountered by reptiles, their brain has responded along with the rest of the body. There is an increase in the size of its parts, with added nervous material where necessary. The activity of the bird requires a great increase in the size of the telencephalon. The olfactory region is reduced, being smaller than in the lower forms. The cerebral lobes are smooth, with no corrugations or furrows. The pallium is thin and not highly developed, but there is an increase in the number of neurons contained and also a number of new connecting tracts. The corpus striatum is much enlarged, and evidently important to the bird from the tracts connecting it with the posterior part of the brain. The lateral ventricles are slit-like, since they are encroached upon by the corpus striatum. As the telencephalon extends posteriorly to meet the cerebellum, the diencephalon and mesencephalon are not evident from the dorsal surface. The pineal body reaches the dorsal level of the brain by extending anteriorly through the angle made by the two cerebral lobes.
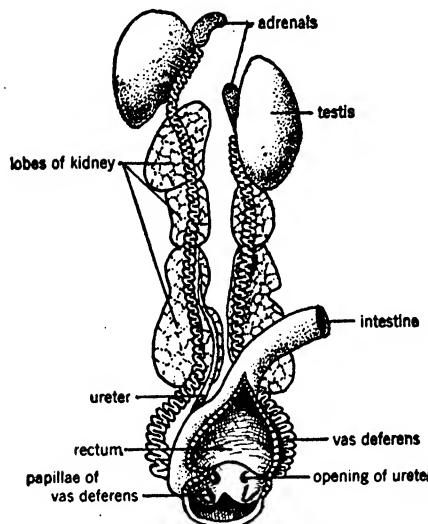
FIG. 312. Male urogenital system of Gallus.
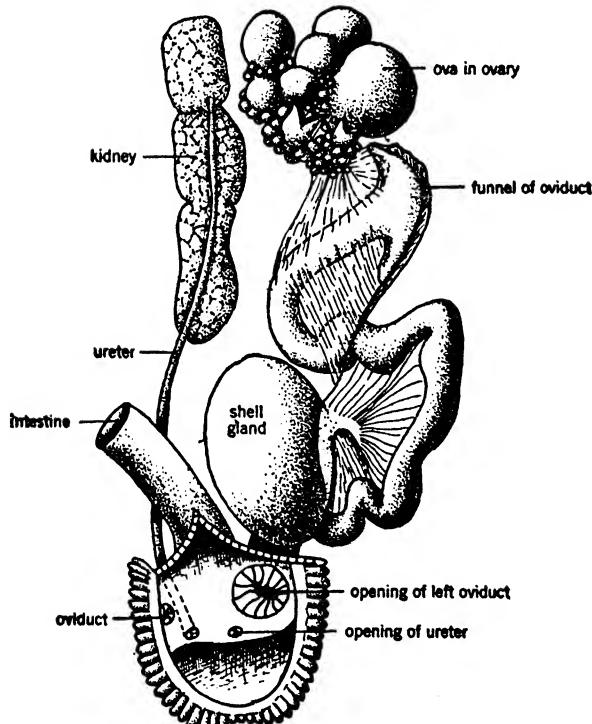
FIG. 313. Female urogenital system of Gallus. Redrawn from Schimkewitsch.

The diencephalon contains the slit-like third ventricle with two openings, the interventricular foramina, leading to the lateral ventricles. The roof is thin, with the epiphysis, or pineal body, extending anteriorly, and the chorid plexus dipping into the ventricle. Ventrally the optic chiasma is just anterior to the infundibulum. The hypophysis is quite distinctive and ventral to the infundibulum. As the side walls must carry most of the tracts leading to the telencephalon, the thalamus is rather thick.

The mesencephalon is also covered by the overgrowth of the cerebellar lobes, and the corpora bigemina are extended out laterally, being larger and even more lateral than in the reptiles. A small tube, the iter, leads through the mesencephalon to connect with the fourth ventricle. The large posterior commissure is on the dorsal border on the anterior part of the roof. The optic nerves have their centers in the corpora bigemina and extend anteriorly from this region to the chiasma.
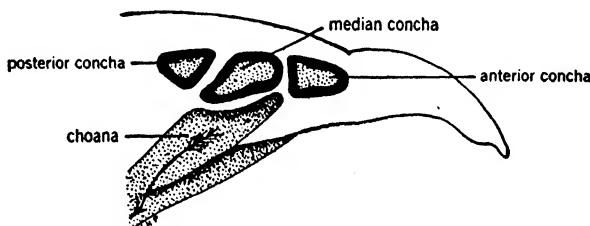
FIG. 314. Sagittal section of nose of Gallus.

The cerebellum of the metencephalon is large and has a pair of flocculi on each side. The dorsal surface of the cerebellum is thrown into ten folds, which increase its area, since the activities of the bird demand a large number of brain cells for equilibrium. The pons is lacking in birds since only a few fibers cross from the sides of the cerebellum.

The medulla oblongata, or myelencephalon, is short, with a prominent flexure and a large fossa rhomboidalis covered by a choroid plexus. It contains the fourth ventricle, and along its sides the last six cranial nerves take origin.

The spinal cord extends to the pelvic region with large plexus for the wings and legs, the thoracic plexus being especially large because of the amount of muscle tissue concerned with flight.

Sense Organs. — The sense of smell seems rather weak in birds and is not used for food-hunting. The air enters the paired nostrils and is drawn over a series of turbinals on the lateral wall of the ethmoid. The olfactory nerve spreads over the olfactory membrane, at the

posterior region of the nasal cavity. The posterior choanae enter the
mouth by a single median slit (Figs. 314, 315).

The eyes (Fig. 234) are extremely keen, since it is upon them that the
birds depend for food and safety. The eye of *Gallus* is fairly typical.
The sclerotic coat is ossified,
forming a series of sclerotic
bones that surround the pupil.
Hawks and owls have the
sclerotic bones formed into a
cup. The lens is held in place
by the ciliary process, which is
attached to the eyeball at the
ora serrata. The iris, with its
circular muscles, is stretched
anterior to the lens and at-
tached to the choroid. The
posterior region of the eyeball
is large and has a distinctive
pecten (Fig. 234) developed at

Fig. 315. Cross-section of nose of Gallus.

the point of entrance of the optic nerve. The pecten extends toward
the lens and is in contact with the ciliary process. The accommodation
of the eye is obtained by the muscles of the iris and ciliary process,
which lie between the cornea and the sclerotic coat. These muscles
pull on the lens and change its convexity.
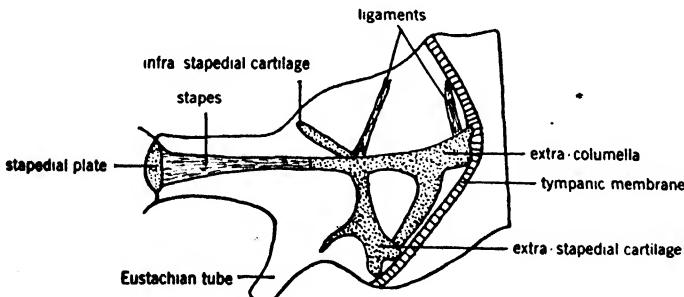
Fig. 316. Middle ear of Gallus. Redrawn from Bütchli.

The ear (Fig. 224) is highly developed, and superior to that of the
reptiles. The whole structure is housed in cancellous bone. The
external meatus, which is always open, is curved so that the tympanic
membrane is well protected, and a glandular worm-like ridge extends
along the floor of the meatus. A few birds (owls) have the outer meatus
provided with movable flaps that serve as pinnae, with a protecting

fringe of hair-like feathers. The tympanic membrane is convex and is held in position by the extracolumella. The middle ear is small and has a permanent Eustachian tube. The tubes unite and open to the roof of the pharynx by a single median slit. The ossicles of the ear consist of the stapes, with its plate fitting snugly into the foramen vestibuli. The columella (Fig. 316) extends as a long slender bone from the stapedial plate, and is continued to the tympanic membrane by the extracolumella, an irregular piece of cartilage which is attached to the tympanic membrane at several places. The ear has a very well-developed lagena, containing an organ of Corti, which evidently does the work of the same organ in mammals. The anterior semicircular canal is large, but the utriculus and the sacculus are rather small in proportion. (See Chapter X.)
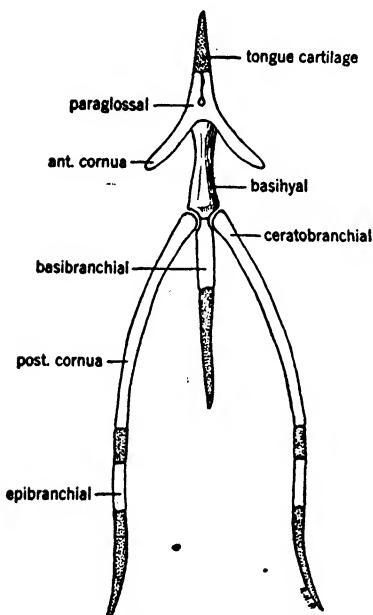
Fig. 317. Tongue bones of Gallus.

Résumé

The first birds (*Archaeopteryx*) appeared in the Jurassic period, originating probably from the same reptilian branch that gave rise to the dinosaurs, pterodactyls, and crocodiles. Birds are primarily flying animals, and every part of their body is adapted to assist in this activity. The outer layer of skin is corneous as in reptiles, but the covering of feathers is unique. The skeleton is noticeably light, the bones being spongy in flying birds but more solid in walking birds. The vertebral column is strengthened by fusion in the thoracic and sacral regions, to form a rigid connection for the pectoral girdle and to permit bipedal locomotion. The individual vertebrae are peculiar, with saddle-shaped centra in modern birds. The vertebrae of the tail are coalesced to form a pygostyle. There is a striking development of the sternum in flying birds, with a keel for the support of flight muscles, while the sternum of walking birds is flat. Both wings and legs are highly specialized and have a reduced number of digits. The skull is somewhat reptilian, the bones being light and having air spaces, and most of them being fused together. Modern birds have no teeth. The digestive tube is well differentiated into regions; the esophagus often has a special development, the crop; the stomach may be divided into a proventriculus and a ventriculus; the length of the intestine varies with the kind of

food; the cloaca is retained as in reptiles. The lungs are relatively large and highly specialized, with six pairs of connecting airsacs which extend to other regions of the body and greatly aid in respiration. The lungs are subdivided by horizontal and perpendicular septa. The glottis is well supplied with cartilages, the arytenoids and cricoids, and the trachea is ringed with cartilage. The syrinx, or sound-producing organ, is at the base of the trachea. The heart is four-chambered, since the ventricle is completely divided. The blood from the head returns through the jugulars, and the blood from the body through the post-cava. The renal portal system still returns the blood through the kidneys, but there is no action there as in fishes and amphibians. There is a complete separation of the sixth aortic arches from the aorta to form the pulmonary arteries, and only the right half of the fourth arch is retained to form the systemic vessel. Birds have a fairly stable temperature, usually much higher than that of mammals. Ductless glands are much better developed in birds than in the lower vertebrates; the thyroid, parathyroid, pineal, hypophysis, adrenals, and gonads supply internal secretions of great importance in the economy of the entire body. The kidneys of birds are of the metanephric type. A urinary bladder is not developed, the ureters emptying directly into the cloaca. The testes discharge their products through the vas deferens, which ends in a papilla that sometimes serves as a penis. Only the left ovary is functional in birds, the right ovary being vestigial. All birds are oviparous. Their nervous system is highly specialized, and the brain is much larger in proportion than that of reptiles. The pallium is thin and not highly developed, but there is an increase in the brain tracts, the corpus striatum, and the cerebellum. The spinal cord is enlarged, to meet the demands of the wings and legs. The nose loses its importance and is rather weak. The eyes, which are much used in food-getting, are well developed, having elliptical lenses and excellent ciliary attachments for focusing. A pecten may be present, and bones may develop in the sclerotic coat. The ear is slightly better than that of reptiles. There is but one ossicle, the stapes, with a columella and extracolumella cartilage for connection with the internal drum. The lagena is highly developed and has an organ of Corti as in mammals.

CHAPTER XVII

MAMMALS

Although the first known fossils of primitive mammals are from the Jurassic, some of the small theromorph reptiles of the Permian and Triassic had many of the characters that were to be utilized in the new mammalian group. Their skeletons were becoming more refined without becoming overspecialized and without losing any of the essential structures for further developments. The brain was enlarging, the growth of the cerebral lobes being foreshadowed by an increase in the size of the pallium. The teeth, instead of being cone-shaped, could now be differentiated into incisors, canines, and molars. The jaws and ears were undergoing modifications that suggested what was to follow later, since the posterior part of the jaw was becoming small and weak, most of the stress being taken by the dentary and its processes. This was to leave the posterior end of the jaw free and in a position to be taken into the ear, along with the reduced quadrate, to form the mammalian incus and malleus. The articulare was also greatly diminished and was moved to the inside of the jaw. The squamosal was enlarged, being extended downward to form the new articulation for the dentary.

Primitive mammals continued to develop through the Mesozoic, although their remains are few and their numbers small. At this time they were in competition with the great reptiles, and their progress was slow at best. With the advent of the Tertiary, when conditions changed, the reptilian groups became greatly reduced or died out altogether, and this was the opportunity for the newly developed mammals. They increased in numbers, and by the middle of the Tertiary most of the modern orders were differentiated and became somewhat similar to their present-day descendants. This was a period of further refinement, when the best seemed to survive, replacing the animals that were not able to meet the changing conditions and climate. Many grotesque forms arose but did not survive. Migrations were common, and there was an interchange of species and groups from continent to continent. During the Pleistocene there was a general reduction in the abundance of practically all orders of mammals. The history of such groups, as the horse, camel, rhinoceros, and elephant, has been very completely reconstructed, so that the development of limbs, teeth, tusks, brain case, and other skeletal parts can be followed from their inception

to their mature form. This has been of inestimable value in determining the exact way in which modern structures have been produced.

Mammals parallel the reptiles in their responses to the variable conditions of land life. They become differentiated into forms suited to changing environments and to various kinds of activities, such as walking, running, jumping, flying, climbing, digging, and swimming, with a further division into carnivorous and herbivorous types, each with its special adaptations. The walking animals are those without any special adaptations of the limbs, either in skeleton or in musculature, and, although they are able to run, walking is their ordinary gait. The running forms are specialized in both skeleton and musculature, with every segment of the limbs elongated and with muscles suitable for active movements. Jumping animals include the kangaroos and the jumping mice and rats, with small fore limbs and greatly enlarged posterior limbs. Arboreal animals are found in many orders. The highest type is the gibbon, with its grasping hands and feet and elongated arms, though many other primates also live in trees. Sharp claws instead of grasping hands and feet are used by many other arboreal animals. Volplaning appears in *Galeopithecus* (Fig. 35), the phalangers, flying squirrels, and others. Digging animals require strong claws and a special development of the skeleton and musculature of the fore limb. The ground is the home of many mammals that use it for protection and safety, and a few, such as moles or gophers, are real subterranean forms, getting their food and spending most of their time under the ground. The cetaceans, including the whales, dolphins (Fig. 40), and porpoises, are the most highly specialized for a water existence, and they need not go to land at any time. Another large series, including the seals, walruses (and sea-cows), live near the shore and depend upon the land for certain phases of their activities, such as the rearing of young. A large number of inland animals find the water very attractive and get most of their food along the lakes and water courses. Some of them, such as beavers and muskrats, cannot exist without a water environment.

With the great increase and spread of man in modern times, the larger mammals have been driven back to the frontiers, except those that have been domesticated and those for which large areas have been set aside under government control and protection. The smaller mammals are better able to continue in spite of man, but even they are becoming restricted, as their natural habitats are changed by continual tilling of the land, draining the swamps, changing the water courses, cutting the timber, over-grazing, and the building of dams. The fate of the mammals rests largely in the hands of man, and the future is doubtful.

The mammals are distinguished from other vertebrates by a number

of characters. Hair is the characteristic epidermal covering on all mammals, although it may be vestigial as in the whales and *Sirenia* (Fig. 42). The mammary glands are unique. The heart is four-chambered as in birds, but the left aortic arch (instead of the right) becomes the systemic vessel. A complete muscular diaphragm separates the lungs and heart from the peritoneal cavity. Sweat and oil glands are present in the skin, which is thicker than in other vertebrates and has a better-defined epidermal layer of living and dead cells. The brain is larger in proportion to the body weight, and marked by new structures that did not appear in the lower groups. The cerebrum is enlarged, the pallium is much thickened, and the new cerebellar lobes make their first appearance. Internally, the brain tracts increase in number, and the whole brain increases in complexity. The teeth are differentiated into incisors, canines, premolars, and molars, and usually the milk dentition is followed by a second or permanent set. The red blood corpuscles are small and without nuclei. There is a reduction of the number of bones in the skull by combinations and eliminations. The condyles are paired as in the Amphibia. The quadrate and articulare are drawn into the ear as the incus and malleus, thus completing the chain of ossicles. The temporal bone is made up of a combination of elements and supplies the articulation for the jaw, thus replacing the quadrate. The jaw consists of the paired dentaries, which may be ankylosed into a single structure or merely joined by a symphysis. The rest of the skeleton is less variable than in the lower forms, with more stability of parts. The formation of the placenta from the allantois is a very striking adaptation in the higher mammals. The temperature regulation is good, and mammals are generally homothermous. The larynx is highly specialized.

ANATOMY OF THE RAT

The rat, *Epimys norvegicus*, which is found all over the world, may serve as an example of the Mammalia, being of small size and showing all the structures needed for the demonstration of mammal characteristics, without being too specialized for our purpose.

Skull. — The skull of the rat is typical of the mammals, with a slight reduction in the number of bones when compared with the reptiles. The squamosal forms the articulation for the lower jaw. The brain case is enlarged. The quadrate has entered the ear as the incus, and the posterior end of the reptilian jaw has contributed the articulare to form the malleus. The pterygoids, very useful in the lower vertebrates, have been reduced to small processes on the posterior end of the palatines. No quadrato-jugal is present, and several other elements

have been lost or combined. Since the openings between the bones of the skull are smaller or entirely absent, definite openings must be formed for the exit of the cranial nerves and for the entrance and exit of blood vessels. Most of these foramina are confined to the ventral and lateral side of the brain case. (See Chapter IV; Figs. 85, 86, 87, 88, 89, 90, 91, 92.)

The dorsal side of the skull is marked by some prominent ridges. The parietal and occipital bones join at right angles, forming the lambdoidal ridge. On each side of the skull, dorsal to the opening for the external meatus in the bulla, a sharp ridge ascends and extends along the side of the skull to the nasal bones. The roof of the skull is wedge-shaped, narrow at the anterior end and gradually widening out as the brain case is reached. The median region is covered by the paired nasals, frontals, parietals, and the single supraoccipital. The side walls of the skull are formed by the premaxilla, maxilla, lacrimal, pre- and orbitosphenoid, basi- and alisphenoid, temporal, and the lateral parts of the occipital. The eye is in a depressed area of the lateral side, the lower border of the orbit being formed by the process of the maxilla, the process from the temporal, and the connecting zygomatic, or jugal. The ventral side of the skull is more irregular than the dorsal, with more openings, since all the foramina are on the lateral or ventral sides. The paired premaxillae form the anterior part, followed by the maxillae, palatines, presphenoids, basisphenoids, and the basioccipital. The small median vomer is in the floor of the nasal cavity, and not seen from the ventral side. The pterygoids, small bones attached to the posterior ends of the palatines, are no longer connected with the temporal region of the skull, having lost their connection when the quadrate was taken into the ear. Their importance is reduced and they remain as vestiges. The bullae, which are expansions of the tympanic bones, are joined with the petrosals, forming a structure which contains the ear mechanism. The three ossicles of the ear connect the foramen vestibuli (ovale) with the tympanic membrane, which is stretched over the opening of the bulla. This part of the temporal is not tightly sutured to the skull. The four occipital bones are combined into one element with a large opening, the foramen magnum, through which the spinal cord extends.

The basicranial region of the rat differs strikingly from that of a reptile. The extension of the maxillae in a mesial shelf forms the hard palate and separates the nasal cavity from the mouth. The quadrate is gone, and with it the chain of elements that braced it to the anterior part of the skull.

A pair of long, narrow slits, the anterior palatine foramina, lie between the premaxillae and palatines. The narial passages open into the

pharynx on the median line posterior to the molars. Numerous small foramina are to be seen on the ventral and lateral sides of the skull. (See Chapter IV, figures of mammalian skulls.)

Mandible. — The dentaries are joined together by a symphysis that permits some movement. The posterior end is expanded to form a surface for the insertion of muscles and for the articulation with the skull, having a dorsal or coronoid process for muscle insertion, a median ramus for articulation with the temporal, and a ventral process at the angle for the insertion of muscles. The teeth in the lower jaw, as in the upper, are separated by a diastema. (See Chapter IV.)

Teeth. — The teeth of the rat are highly specialized and of the rodent type. The incisors, four in number, have open roots and grow throughout the life of the animal. They are chisel-shaped and self-sharpening. The molars are ridged to form a grinding surface, and suited principally for a vegetable diet. The pattern of the molars is very useful in the classification of the rodents. The tooth formula is $\dfrac{1\text{-}0\text{-}0\text{-}3}{1\text{-}0\text{-}0\text{-}3}$.

Visceral Skeleton. — The visceral skeleton (Fig. 98) is reduced to the hyoid bone, a U-shaped structure, consisting of a body and two cornua, a greater and a lesser.

Vertebral Column. — The axial skeleton consists of a number of vertebrae divided into regions, each region having certain characteristics and arranged as follows: cervicals 7, thoracics 13, lumbars 6, sacrals 4, caudals 24+ .

The cervicals are modified for the work that they have to do in supplying a support for the skull and in giving pliability to the neck. The typical cervical vertebra consists of a centrum, a neural arch and spine, and articulating processes. The articulating face of each prezygapophysis points dorsally, and that of the postzygapophysis ventrally. The transverse process on each side of the centrum has a foramen for the vertebral artery at its base. The neural arch is shorter than the centrum, so that the spinal cord is not completely roofed over, thus giving more movement. The ends of the centrum are acoelous, or flat, as in most mammals. The first two vertebrae, the atlas and the axis, are the most specialized. The atlas is ring-shaped and without a centrum, but with two facets on the anterior face that articulate with the condyles of the skull. It is made conspicuous by wing-like lateral processes. The axis, or epistropheus, is characterized by a large neural spine and an odontoid process, which is all that remains of the centrum of the atlas.

The thoracic vertebrae are marked by dorsal spines, the first being almost perpendicular and the rest inclining gradually more to the

posterior. These spines are for muscle insertions and for the attachment of tendons from the head region. The facets on the anterior and posterior regions of the centra are for the capitular and tubercular heads of the ribs, respectively.

The lumbars gradually increase in size from the first to the last. Their spines are inclined anteriorly with a gradual increase of the inclination as the last vertebrae are reached. The centra are large, much heavier than in the thoracics, with large transverse processes. The hypapophyses, median flanges on the ventral surface of some of the lumbars, are similar to those developed in birds and reptiles.

The sacral vertebrae have short neural spines. The first two have transverse processes articulating with the pelvis and may be called the true sacrals, whereas the other two resemble caudals.

The caudal vertebrae number from twenty-four to twenty-eight. The first of the series are like other vertebrae, but there is a gradual loss of parts until they finally become rod-like with no recognizable processes. A few may have chevron bones on the ventral side.

Ribs. — The ribs are thirteen in number, each with a capitular and a tubercular head. The first seven articulate with the sternum by semi-ossified costal cartilages; the last six are joined by cartilage only.

Sternum. — The sternum (Fig. 108) consists of six sternebrae, the first keeled and expanded at the anterior end, and the other five rod-like. The last segment, the xiphisternum, ends in cartilage. The clavicle articulates with the first sternebra.

Shoulder Girdle. — The shoulder girdle consists of the scapula and clavicle (Fig. 112). The scapula inclines slightly to the posterior, and its dorsal edge projects above the spinal column, this making a slight elevation on the body. The body of the scapula is triangular, and its inner surface is comparatively smooth, with slight fossa for muscle insertion. The outer face is marked by the large spine which is drawn out ventrally into a large acromion process. The glenoid cavity on the ventral face is overhung by the hook-shaped coracoid process, all that remains of the coracoid bone. The clavicle is a small S-shaped bone that articulates with the coracoid process of the scapula and with the manubrium of the sternum.

Anterior Limb. — The proximal segment of the fore limb has a single bone, the humerus. Its proximal end has a large head which articulates with the glenoid cavity, a greater tuberosity which is continued down the length of the shaft as the deltoid ridge, and a lesser tuberosity that is mesial on the head. The groove for the tendon of the biceps is between the two tuberosities. The distal end is developed into a trochlea for the articulation of the radius and ulna. The posterior

face of this distal end has a deep fossa for the olecranon process of the ulna.

The ulna is post axial, articulating with the humerus by a deep sigmoid notch, which is followed by the olecranon process. It has a small notch distal to the sigmoid for the articulation with the head of the radius. It articulates with the carpus through the ulnare, or triquetral. The radius is preaxial, rod-like, and decidedly curved. Proximally, it articulates with the humerus and ulna, and distally with the radiale. Through its articulations and musculature the radius is able to perform a twisting movement. (See Chapter IV, Figs. 112, 114, 115.)

Carpus. — The carpus consists of a proximal row of four bones, the radiale (scaphoid), intermedium (semilunar), ulnare (triquetral), and pisaform (sesamoid); a distal row of four bones, carpale 1 (trapezoid), carpale 2 (trapezium), carpale 3 (capitatum), and carpale 4 + 5 (hamatum); and the centrale, a small bone wedged in between the intermedium and the distal row, representing a third row once present in the carpus.

Metacarpus. — The five metacarpals articulate with the four carpals proximally and with the five digits distally. The fourth and fifth digits articulate with the combined carpal 4 + 5. The first finger or pollex has two phalanges, the rest three, which is the typical mammalian formula: 2-3-3-3-3. Each has a typical claw except the first which is nail-like.

Pelvic Girdle. — The pelvic girdle (Fig. 102) consists of a pair of combined elements that are articulated with the sacral vertebrae. Since most of the weight comes on the hind limbs, this articulation is always well made. Ventrally, the pelvic bones join by a symphysis but are not ankylosed as in some mammals. Each half of the girdle consists of three bones, the ilium, pubis, and ischium. The obturator foramen is formed by the joining together of the pubis and ischium. All three bones assist in the formation of the acetabulum, into which the head of the femur extends. The proximal end of the pubis ossifies separately on the rim of the acetabulum and is called the cotyloid bone.

Hind Limb. — The posterior limb consists of the same number of segments as the anterior. The first segment is formed by the femur (Fig. 123), a large heavy bone with a mesially extended neck and head which fits into the acetabular cavity. There are three trochanters for muscle attachments: the greater trochanter on the proximal head, a lesser on the inner side, and a third on the outer side of the shaft. The distal end has two condyles which articulate with the tibia. Between these condyles is a smooth groove for the patella, which is a sesamoid

bone developed in the tendons. Two small fabellae, also sesamoid, are found just posterior to the knee joint.

The second segment has two bones, the tibia and the fibula (Fig. 124). The main part of this segment is formed by the tibia, however, since the fibula is ankylosed to the distal third of the shaft and is free only on the upper two-thirds. The tibia is large and has a sharp anterior edge, the cnemial crest. The proximal end articulates with the femur, and the distal end with the astragalus (talus). The small free end of the fibula also has a slight articulation with the astragalus.

Tarsus. — There are eight bones in the tarsus. The proximal row consists of the fibulare (calcaneus) and the tibiale (talus or astragalus). The distal row consists of four bones, as follows: tarsale 1 (first cuneiform), tarsale 2 (second cuneiform), tarsale 3 (third cuneiform), and tarsale 4 + 5 (cuboid), the last being a fused pair. The single centrale (navicular) lies between the astragalus and the first three tarsals. The metatarsus consists of five elongated bones forming the foot and each supporting one toe except tarsale 4 + 5 which supports two. The digital formula, 2-3-3-3-3, is the same as in the anterior limb. All the toes are equipped with claws. (See Chapter IV.)

Digestive System

The mouth opening is slightly ventral and posterior to the narial openings. The large incisors are separated from the molars by a diastema, into which the sides of the mouth press so as to separate partially the anterior from the posterior part. The roof is strongly corrugated, having three heavy ridges at the anterior end, and five slight, W-shaped ridges between the molar teeth. The mouth is well supplied with glands (Fig. 138) of several types, so necessary in masticating dry food. The large parotid gland, anterior to the ear, extends ventrally, almost to the median line of the neck, and opens into the mouth through Stenson's duct. The large submaxillary glands, on the median side of the neck at about the angle of the jaw, send their product to the mouth through Wharton's duct. The sub- and retrolingual glands are located anterior to the submaxillaries. The large suborbital glands open into the roof of the mouth. The different glands supply the saliva and the fluids for lubrication. The fleshy tongue is covered with small papillae, giving it a smooth, velvety appearance. The tongue is attached to the skull through the hyoid bone.

The short pharynx connects the mouth with the esophagus. Opening into it are the narial passages, the Eustachian tubes, and the glottis.

The U-shaped stomach (Fig. 318) lies between the lobes of the liver.

Both the entrance and the exit are at about the middle of the concave dorsal wall. The cardiac region is thin walled and semi-transparent; the pyloric end is heavy and much thicker, with a conspicuous ridge separating it from the cardiac portion. The exit, through the pylorus, is protected by a sphincter muscle. The digestive juices of the stomach
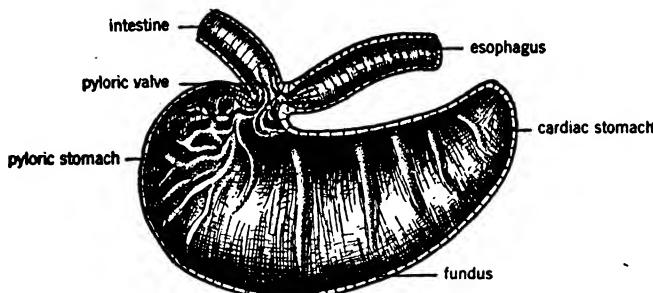
FIG. 318.   Stomach of white rat.

are supplied through the glands in the pyloric region. The stomach and the rest of the digestive tube are made up of the four typical layers, the mucosa, submucosa, muscle, and serosa.

The duodenum starts at the pyloric end of the stomach, and ends where the liver and the pancreas discharge their products through a common duct. It forms a loop in which the pancreas lies.
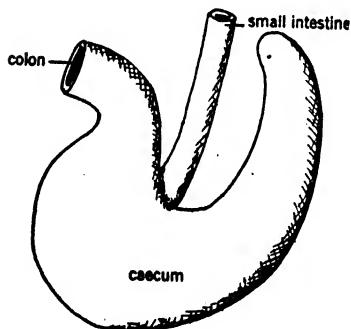
FIG. 319.   Caecum of intestine of white rat.

The jejunum and ileum may be considered as one section, since the separation is not evident in the rat. It is in this section that most of the digestion and absorption takes place, and the inner wall is well supplied with villi, Peyer's patches, and lymph nodes. The ileum ends in the iliocolic valve. The food, after passing through this valve, enters a slight chamber from which it has the possibility of entrance either to the colon or to the caecum.

The caecum (Fig. 319) is shaped somewhat like the stomach, is thin walled with some thickened areas for absorption, and is generally filled with a fine material after a meal.

The wall of the colon is alternately thick and thin, so that its internal surface has conspicuous folds. Its function is to extract water from the feces and to form the excreta into small pellets for discharge through the anus.

The liver (Fig. 320), which almost encircles the stomach, is divided into five lobes. The organ is held in place by a suspensory ligament, attaching it to the diaphragm. No gall bladder is present, and the bile enters the distal end of the duodenum through a duct which winds through the mesentery and unites with the ducts from the pancreas before entering the digestive tube. The pancreas is a many-lobed organ lying in the loop of the duo-
denum.

FIG. 320: Liver of white rat.

The spleen, a conspicuous brown organ, lies along the left side of the stomach. It has nothing to do with digestion, however, since it is a lymph gland and is associated with circulation.

The whole digestive tube is held together by the mesenteries, thin folds of the peritoneum, that are attached to the dorsal midline of the peritoneal cavity. These mesenteries contain blood vessels, lymph glands, lacteals, and vessels connected with digestion.

Respiratory System

The lungs (Fig. 321) and their associated structures reach a high stage of development in the mammals. The larynx and trachea become highly specialized by the addition of parts and by the improvement of the old structures. As in the birds, the lungs are sponge-like and filled with alveoli. By the completion of the diaphragm, they are now enclosed in pleural sacs and completely separated from the viscera, so that they have more protection and lubrication. The diaphragm, which is muscular, functions in breathing. The abdominal and intercostal muscles, by which the ribs are moved and the capacity of the chest changed, also aid in breathing.
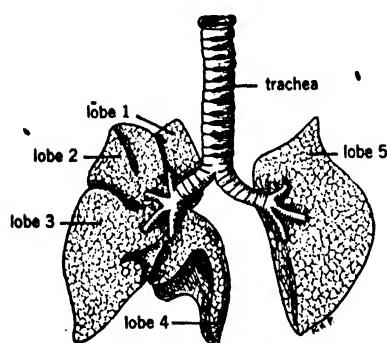
FIG. 321. Lungs and trachea of white rat.

In the rat the air, coming through the narial passages, is taken through the glottis, larynx, and trachea to the lungs. The larynx consists of five cartilages, two cricoid, two arytenoid, and the single median thyroid across the ventral side, the Adam's apple of the human. The entrance

to the glottis is protected by a mucus-covered cartilage, the epiglottis, which prevents the entrance of food. The vocal cords are stretched across the arytenoid cartilages. The thyroid glands are closely appressed to the sides of the larynx and are connected by a thin strand. The trachea is surrounded by incomplete rings of cartilage. Between the lungs it divides into two bronchii, which subdivide into secondary and tertiary bronchii. The left lung consists of one lobe and the right of four. (The finer structure of the lung is described in Chapter VIII, on respiration.)

Circulatory System

The circulatory system of the rat is representative of the high type found in the Mammalia. The erythrocytes, or red blood corpuscles, are very small and non-nucleated. The heart (Fig. 156) is four-chambered, consisting of two atria and two ventricles. The atria are thin walled and have ear-like appendages, the auricles; the ventricles are heavy-walled, the left being much larger than the right. The left aortic arch is the systemic vessel. The atrio-ventricular valves are the tricuspid on the right and the bicuspid, or mitral, on the left. These valves are formed from flaps of tissue supplied with chordae tendinae and papillary muscles to hold them against the back pressure when the ventricles contract. The outgoing vessels are supplied with pocket (semilunar) valves. The beating of the heart is synchronized by the bundle of His, a strip of neuro-muscular tissue imbedded in the wall separating the two sides of the heart. The mammalian heart is practically a double pump, with no interconnecting vessels of any kind. Blood for the nourishment of the heart comes to it through the coronary arteries.

The right atrium receives all of the venous blood returned from the body. The right anterior vena cava enters dorsally, the left anterior vena cava enters ventrally and mesially, and the postcava enters ventrally. Between the entrances of the first two cavae is a fold of tissue, the valvula venae cavae.

The blood from the right atrium enters the right ventricle through the tricuspid valve, which consists of three folds of tissue that extend into the ventricle. Each fold is anchored to the walls of the ventricle by numerous chordae tendinae, each with its papillary muscle.

The right ventricle is thin walled, since it does nothing but force the blood through the pulmonary arteries to the lungs. The opening from the right ventricle to the pulmonary arteries is on the dorsal wall and is protected by three semilunar valves.

The left atrium is thin walled and has only one inlet, since the two pulmonary veins unite before entering. Its outlet is through the

mitral, or bicuspid, valve, which is also attached to the walls of the ventricle by chordae tendinae and papillary muscles.

The left ventricle is much heavier than the right, since it must force the blood over the whole body. The entrance to the aorta is protected by three semilunar valves. (See Chapter VII.)

The aorta, after leaving the ventricle, curves to the left and descends along the back wall of the body cavity, giving off branches to the different organs and structures (Fig. 322). The coronary, to supply the heart itself, comes off at the base of the aorta. The right innominate is divided to form the right subclavian and the right carotid. The left carotid is not united with the left subclavian, each coming off singly. The coeliac, the first branch below the diaphragm, supplies the spleen, liver, stomach, and the other anterior parts of the digestive system. The anterior and posterior mesenterics supply the remaining parts of
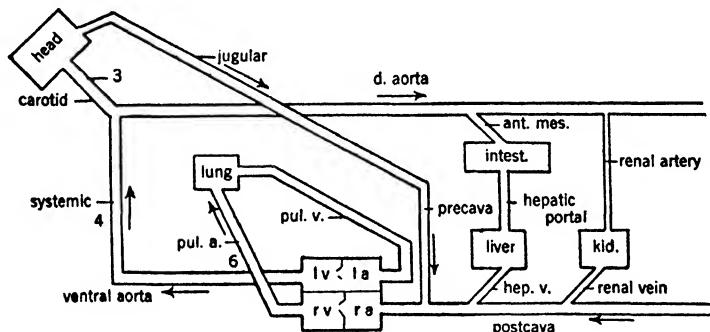
FIG. 322. Diagram of mammalian circulation.

the digestive system. Small vertebral arteries extend from the aorta along most of its length to supply the walls of the body. The gonads and kidneys have their individual arteries. Small iliolumbar arteries supply the muscles of the lower back. Finally the aorta divides into two branches, the right and left iliacs, which supply the two hind limbs, (Fig. 169).

The blood from the anterior part of the body and head region enters the right atrium by two precavae, each formed by the union of a jugular and a subclavian. The large postcava enters the atrium independently of the precavae. The postcava begins posteriorly by the joining of the right and left iliac veins, which bring the blood from the two hind limbs and caudal region. Small iliolumbars drain the posterior back muscles, and vertebral veins enter along the entire length of the postcava. Each gonad and kidney has its independent vein. The hepatic vein, coming from the liver and returning the blood from the intestines, enters the postcava near the diaphragm (Fig. 175).

Urogenital System

Kidneys. — The kidneys (Fig. 323) of the rat are paired structures, on the posterior wall of the coelom, not in the coelomic cavity, but shut
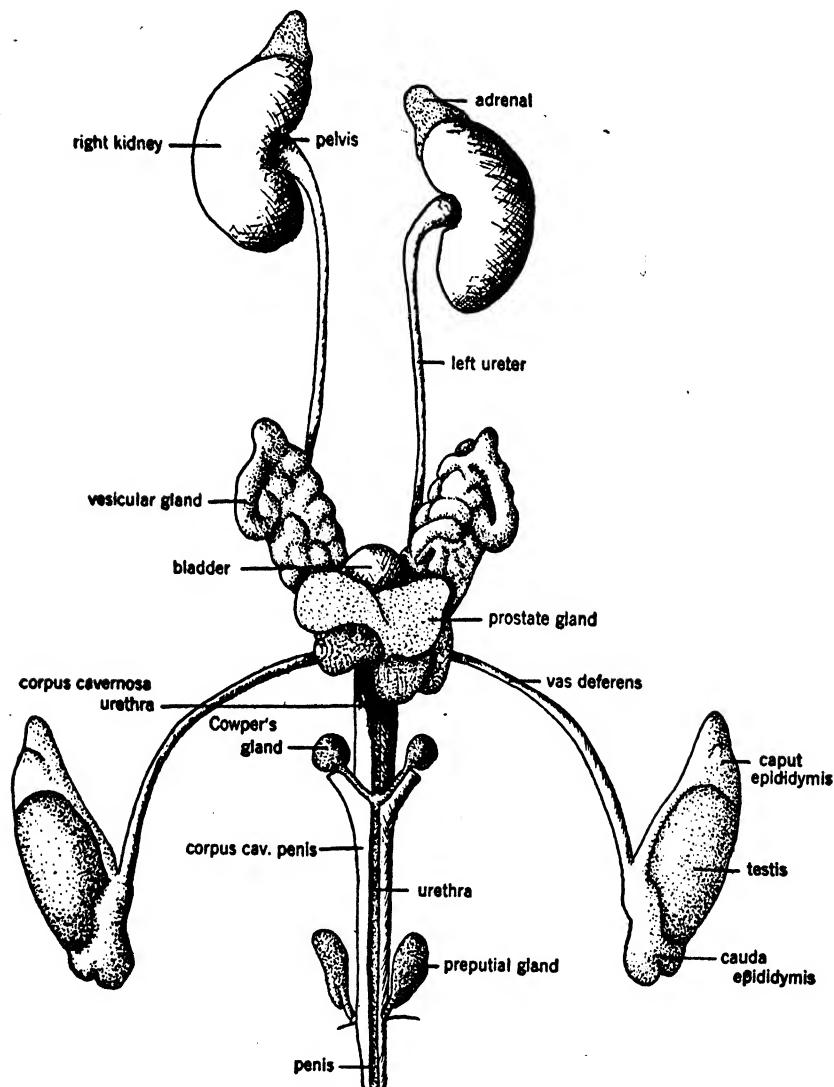
FIG. 323. Urogenital system of male white rat.

off from it by the peritoneal lining. There is a small ductless gland (the adrenal) on the dorsal end of each kidney. The right kidney is slightly anterior to the left. The urine from each kidney is carried by a

ureter from the hilum to the dorsal side of the bladder (Fig. 244). From the bladder the urine is led to the outside of the body through the urethra, which in the male is taken through the penis and in the female to a separate opening at the ventral border of the vagina. (See Chapter XI.)

Male Reproductive Organs. — The testes (Fig. 323) are not in the body cavity as in lower vertebrates but in a scrotum. In very young rats they have their original position, and later they descend through the inguinal canals to the scrotal sac. This descent of the testes makes the vas deferens curve over the ureters to reach the urethra. The epididymis forms a cap on each end of the testis, and from it the vas deferens conducts the spermatozoa to the opening into the urethra. The penis consists of two lateral corpora cavernosa and a ventral corpus cavernosum, which contains the urethra. These bodies trap the blood in their loose tissues and become erectile. The penis is attached to the symphysis of the ischia.

The male has numerous glands of physiological importance that assist in delivering the spermatozoa (Fig. 323). The preputial glands, at the end of the penis, open into the border of the prepuce. The prostate glands,

FIG. 324. Urogenital system of female white rat.

opening into the urethra at the base of the bladder, consist of a pair of lobes at each side and a mass surrounding the proximal end of the urethra. This is a lubricating gland that forms the greater part of the fluid in which the spermatozoa are carried. Anterior to the bladder are two large vesicular glands, which also open into the proximal end of the urethra. On the sides of the vesicular glands are another pair, the ampullary. Cowper's glands add their secretion to the seminal fluid, where the urethra joins the penis.

Female Urogenital Organs. — The female reproductive system is not so complicated as that of the male. The kidneys (Fig. 324) have the

same relative position as in the male, but the bladder lies ventral to the vagina, the ureters curving around it to reach its base. The vagina is short and bifurcates into separate Müllerian ducts, which are thickened at their bases to form the two uteri. The uteri are held in place by the broad ligament. The ovaries are small, dark organs, one on each side, and are held in place by the mesovarium. The ova break through the walls when ripe, each leaving a scar, the corpus luteum, which remains for some time on the ovary, as a distinguishing mark. The ova are received by the funnels of the Fallopian tubes, through which they descend to the uteri. Fertilization takes place in the Fallopian tubes, the zygotes being formed by the union of the ova with the spermatozoa, which have worked their way up from the vagina. The zygotes become attached to the walls of the uteri, where the embryos develop. Most of the reproductive glands present in the male are lacking in the female. The clitoris is the homolog of the penis, and a pair of lateral glands seems to be homologous to the preputial glands of the male. (See Chapter XI.)

Nervous System

Brain. — The brain of the rat (Fig. 325) is characteristically mammalian, showing all the structures belonging to this class, though it lacks the convolutions found in the highest mammals. It is relatively larger than that of birds and reptiles and has some additional structures. The telencephalon is greatly thickened, by the growth of the pallium. The cerebellum has developed two new lobes, with a connecting commissure, the pons. The corpus callosum, the major connection between the cerebral lobes, is a new development, and many other connecting tracts are developed, so that the cerebrum becomes the dominant part of the brain, with centers concerned in every activity of the animal. The cerebral lobes are so much enlarged that they completely cover the diencephalon and mesencephalon. The optic lobes now number four instead of two, since the corpora bigemina have divided, forming the corpora quadrigemina. The covering of the brain is in three layers: the outer layer, or dura mater, which lines the brain case, is tough and fibrous; the middle layer, arachnoid, is light and vascular; and the inner layer, or pia mater, is applied closely to the brain, in contact with all its surface.

The dura dips down between the lobes of the cerebrum, forming a thin plate, the falx cerebri, which may become osseous. The dura also dips down between the cerebrum and cerebellum forming another dividing plate, the tentorium, which also may become osseous. Four ven-

tricles are present, two in the cerebral lobes, one in the diencephalon, and one in the myelencephalon.

The telencephalon (Fig. 325) is smooth and has a distinct olfactory lobe at the anterior end. In sagittal section, the corpus callosum, a new structure connecting the cerebral lobes, is quite prominent, and the septum pellucidum and the fornix also appear clearly. The anterior commissure is located at the lower end of the fornix. The inter-ventric-
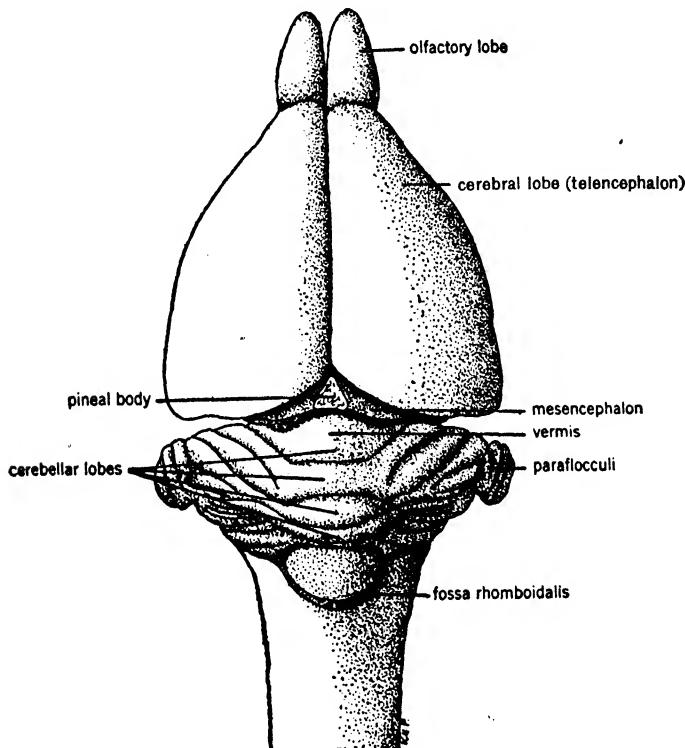
FIG. 325. Brain of white rat. Dorsal.

ular foramen (foramen of Monro) is a narrow slit, located at the ventro-posterior region of the fornix, and connects the third ventricle with the lateral ventricles. The tracts connecting the posterior part of the brain are not conspicuous in a sagittal section but appear in stained cross-sections. The corpus striatum, in the ventral region of the telencephalon, is much smaller than in birds.

The diencephalon (Fig. 326) does not appear in a dorsal view but is clearly defined in sagittal section. Its antero-ventral region is the exit of the optic nerves. Posterior to the chiasma, the infundibulum extends

as a blind pouch along the ventral surface and is surrounded by the hypophysis. On the dorsal wall, a long slender epiphysis, the pineal body, extends between the cerebral and cerebellar lobes. The posterior commissure marks the separation of the diencephalon and mes-encephalon. Extending through the slit-like third ventricle is a large soft commissure, the commissure mollis. Most of the connecting tracts must pass through the walls, or thalami, to get to the different parts of the brain.

The mesencephalon (Fig. 326) is also covered, so that it is not visible from the dorsal surface. The dorsal wall is divided into four lobes, the corpora quadrigemina, concerned originally with the sense of sight but now also a center for the sense of smell. The iter is a small tube connecting the third and fourth ventricles. The ventral region forms the
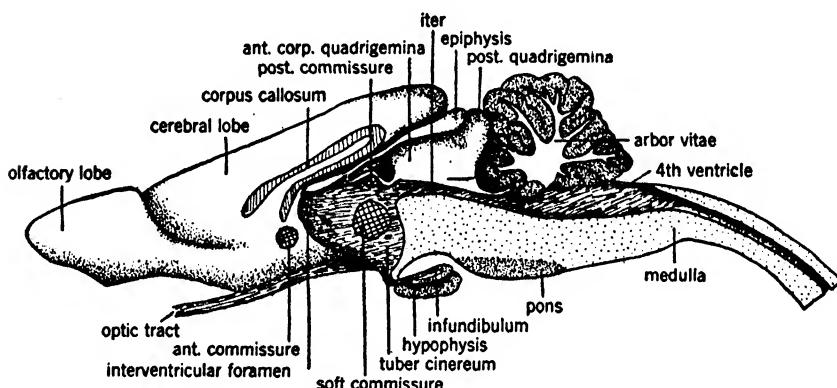
Fig. 326.   Brain of white rat, sagittal section.

brain stem for the transmission of the tracts passing through it. A thin velum separates the dorsal wall from the cerebellum.

The metencephalon (Fig. 325) is a large structure, as in birds. Two new cerebellar lobes have been added, making this division different from all other vertebrates below the mammals. The cerebellum consists of the vermis, the new cerebellar lobes, the lateral flocculi, and the mushroom-like paraflocculi, which extend into a pocket in the side of the brain case. The pons is a U-shaped band connecting the two halves of the cerebellum. The connection with the mesencephalon is by means of a pair of anterior peduncles, and the connection with the myelencephalon is by means of a pair of posterior peduncles.

The posterior medullary velum separates the metencephalon from the myelencephalon. The large fossa rhomboidalis is covered by a choroid plexus, which extends down into the fourth ventricle and forward under the cerebellum. The posterior peduncles must curve around the fossa

to reach the cerebellum. Centers controlling respiration, circulation, and digestion are in this section of the brain.

There are twelve pairs of cranial nerves, as in all mammals. (See Chapter IX for details of cranial nerves.)

The sympathetic system requires only brief mention here, since it is small in the rat and can be seen much better in a larger animal. Careful dissection, however, will show the main parts of the system, the two trunks extending along the vertebral column, inside of the body cavity. Through the visceral branches of the spinal nerves, this system is connected with the central. (See section on sympathetic system, Chapter IX.)
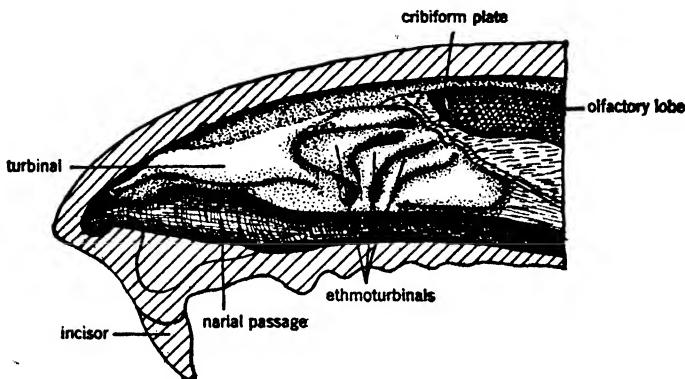
Fig. 327. Nose of white rat, sagittal section.

Sense Organs

The nose (Fig. 327) is well developed, and the sense of smell is keen in all rodents. The olfactory tract extends from the telencephalon to the cribiform plate, through which the olfactory nerves extend to spread themselves over the membrane in the posterior region of the nose. The inside of the nose is arranged in a scroll, in which the air is drawn over moist membranes before it reaches the posterior choanae. The sides of the maxillae form a thin-walled structure, the maxillo-turbinals, and the median posterior region is developed into the ethmo-turbinals. The organs of Jacobson, accessory structures connected with the nose, are present in the hard palate. (See Sense Organs.)

Taste buds are found at the base of the tongue around the circumvallate papillae and probably on the epiglottis. They can be seen in sections of the tongue.

The eye (Fig. 235) of the mammal is slightly different from that of reptiles and birds, since there is no pecten, no sclerotic bones, and only a

vestigial nictitating membrane.   The eyelashes are protective structures, at the bases of which the Meibomian glands supply an oily secretion to the lacrimal fluid.   The lacrimal glands, on the outer border of the eyes, supply the lacrimal fluid for lubrication.

The ear (Fig. 225) has a number of new features, not found in the lower vertebrates.   The middle ear has three ossicles, two of which are new, the incus developed from the quadrate, and the malleus from the articulare.   The lagena, rather straight in the lower forms, now becomes coiled like a snail shell and is called the cochlea.   This contains the organ of Corti, a very complicated mechanism, by means of which the higher qualities of sounds are distinguished.   The periotic bone, surrounding the ear, is the hardest tissue in the animal body.

Many other forms of sense organs are found in different parts of the body, consisting of specialized cells that are used for very definite purposes.   The skin has a number of kinds of nerve endings that interpret only one type of a stimulus, such as heat, cold, pressure, etc. Inside the body and in the supporting tissues are cells that record changed conditions.

Résumé

Mammals first appeared in the Jurassic period, and their ancestry seems to have been through the mammal-like reptiles of the preceding periods.   Hair is the most characteristic external feature.   Sweat and oil glands are present in the skin.   The skeleton is well organized, with the limbs well under the body in contrast to the reptiles.   The axial skeleton is well divided into regions, with a characteristic atlas and axis forming the first two cervical vertebrae.   The anterior girdle, which is reduced in all but the monotremes, consists primarily of a scapula, with or without a clavicle.   The skull has lost some of its reptilian elements, and its structure is quite constant throughout the mammals. The most striking changes are those involved in the new articulation of the mandible through the squamosal bone and the addition of ossicles derived from the quadrate (incus) and the articulare (malleus).   The mandible consists of the dentary bones.   The visceral arches are represented in the hyoid series.   Teeth are present only on the premaxillary, maxillary, and dentary bones and are divided into four types: incisors, canines, premolars, and molars.   A hard palate, formed by the palatines and maxillae, separates the nasal cavity from the mouth, and nasal scrolls are highly developed.   The digestive system is highly differentiated.   No cloaca is present in placental mammals.   The lungs are sponge-like and lie in pleural sacs, separated from the body cavity by the diaphragm, which assists the intercostal and abdominal muscles in inhalation and exhalation.   The larynx has an additional cartilage, the thyroid, and the vocal cords are stretched from the thyroid to the arytenoids, forming the sound-producing structures.   The epiglottis, a new structure, forms a flap over the entrance to the glottis.

The trachea is strengthened by incomplete rings of cartilage. The heart is four-chambered as in birds. The erythrocytes are non-nucleated. There is a tricuspid valve between the right atrium and the right ventricle, and a bicuspid, or mitral, valve between the left atrium and the left ventricle. The left side of the heart has thicker, stronger walls than the right, as the left aortic arch is the systemic artery. Blood from the head enters the heart through the jugular system, and blood from the posterior end through the postcava. The kidneys are compact and are typically bean-shaped. The bladder empties through the urethra. A penis is present in males; the testes may be inside the body or suspended in a scrotal sac; the vas deferens empties into the urethra, close to its exit from the bladder; and connected with the reproductive system are numerous glands that contribute to the seminal fluid. All mammals but the monotremes develop a distinct vagina; the uterus may be double (primitive) or single; the ovum of placentals is very small (0.23 mm.). Reproduction in mammals is of three types: the laying of eggs, as in the monotremes; the bearing of the young in a comparatively rudimentary condition, as in the marsupials; and the development of the young attached to the wall of the uterus by a placenta, which was derived from the allantois. The mammal brain is characterized by the much greater proportionate size and striking development of the cerebrum. The roof of the telencephalon is thick, forming the cerebral hemispheres, which are connected by a new commissure, the corpus callosum. The corpora bigemina of the lower forms are divided transversely to form the corpora quadrigemina. The cerebellum has two additional hemispheres and a new commissure, the pons. The eyes have elliptical lenses and are capable of focusing for widely different ranges of vision. The ear is different from that of all other vertebrates in that three ossicles are present in the middle chamber. There is a marked specialization of the lagena into a coiled cochlea, with its organ of Corti.

BIBLIOGRAPHY

A partial list of the books used in the preparation of this volume, together with others of more general zoölogical interest. Original papers have not been listed, since they are available in the large handbooks of zoölogy and in the regular bibliographical indexes.

ABEL, O. Palaeobiologie. Stuttgart. E. Schweizerbart'sche Verlagsbuchhandlung. 1912.

ABEL, O. Stämme der Wirbeltiere. Berlin. W. de Gruyter and Co. 1919.

ALLEN, EDGAR. Sex and Internal Secretions, A Survey of Recent Research. Baltimore. Williams and Wilkins Co. 1932.

AREY, L. B. Developmental Anatomy. Phila. P. Blakiston's Son and Co. 1930.

AVEBURY, RT. HON. LORD. Prehistoric Times. N. Y. Henry Holt and Co. 1903.

BAITSELL, GEORGE A. The Evolution of the Earth and Man. Yale Univ. Press.

BARBOUR, THOMAS. Reptiles and Amphibians. Boston. Houghton Mifflin and Co. 1926.

BEDDARD, F. E. Mammalia. Cambridge Natural History. Vol. X. 1902.

BEDDARD, F. E. Whales. G. P. Putnam's Sons. 1901.

BEEBE, C. W. The Bird, Its Form and Function. N. Y. Henry Holt and Co. 1904.

BEER, G. R. de. Vertebrate Zoology. London. Macmillan and Co. 1928.

BERRY, E. W. Paleontology. N. Y. McGraw-Hill Book Co. 1929.

BÖKER, HANS. Einfuhrung in die vergleichende biologische anatomie der Wirbeltiere. Jena. G. Fischer. 1935.

BOLK, GÖPPERT, KALLIUS, LUBOSCH. Handbuch der vergleichenden Anatomie der Wirbeltiere. Berlin. Urban und Schwarzenberg. 1931.

BOULE, MARCELLIN. Fossil Men. Edinburgh. Oliver and Boyd. 1923.

BOULENGER, E. G. Reptiles and Batrachians. N. Y. E. P. Dutton and Co. 1914.

BRONN, H. G. Klassen und Ordnungen des Thierreiches. Leipzig. Volumes on vertebrates. 1859.

BROOM, RICHARD. Origin of the Human Skeleton. London. H. F. and G. Witherby. 1930.

BUICK, THOMAS L. The Mystery of the Moa. New Zealand. The New Plymouth. 1931.

BURKHOLDER, J. F. Anatomy of the Brain. (Sheep.) Chicago. G. P. Englehard and Co. 1912.

BURRELL, HARRY. The Platybus. Sidney, Australia. Angus and Robertson, Limited. 1927.

BÜTCHLI, O. Vorlesung über vergleichende Anatomie. Leipzig. Englemann. 1910.

CLELAND, H. F. Our Prehistoric Ancestors. N. Y. Harper and Brothers. 1937.

CURRAN, C. H. Snakes and Their Ways. N. Y. Coward, McCann. 1928.

DANIEL, J. F. The Elasmobranch Fishes. Berkeley. Univ. of Calif. Press. 1928.

DEAN, BASHFORD. Fishes, Living and Fossil. London. Macmillan and Co. 1895.

DERCUM, F. X. The Biology of the Internal Secretions. Phila. W. B. Saunders and Co. 1924.

DITMARS, RAYMOND. The Reptile Book. Doubleday, Page and Co. 1907.

DITMARS, RAYMOND. Reptiles of the World. Sturgis and Walton Co. 1922.

EVANS, A. H. Birds. Cambridge Natural History. Vol. IX. 1900.

FLOWER, W. H., and R. LYDEKKER. An Introduction to the Study of Mammals, Living and Extinct. London. 1891.

GADOW, HANS. Amphibia and Reptilia. Cambridge Natural History. Vol. VIII. 1901.

GOODRICH, E. S. Structure and Development of Vertebrates. London. Macmillan and Co. 1930.

GOODRICH, E. S. Treatise on Zoology. Pt. IX. Vertebrate Craniata. London. Macmillan and Co. 1909.

GREEN, EUNICE CHACE. Anatomy of the Rat. American Philosophical Soc. Phila. 1935.

GREGORY, W. K. The Origin and Evolution of Human Dentition. Baltimore. Williams and Wilkins Co. 1922.

GREGORY, W. K. Our Face from Fish to Man. N. Y. G. P. Putnam's Sons. 1929.

GREGORY, W. K. Man's Place among the Primates. Oxford Press. 1934.

GROEBBELS, FRANZ. Der Vogel. Berlin. Gebrüder Borntraeger. 1932.

GÜNTHER, ALBERT. A Study of Fishes. Edinburgh. Adam and Charles Black. 1880.

HARMER, HERDER, BRIDGE, BOULENGER. Fishes and Ascidians. Cambridge Natural History. Vol. VII. 1904.

HEGNER, R. H. College Zoology. N. Y. Macmillan Co. 1929.

HEILMANN, G. The Origin of Birds. London. Witherby. 1926.

HERRICK, C. J. Neurological Foundations of Behavior. N. Y. Henry Holt and Co. 1924.

HERRICK, C. J. An Introduction to Neurology. Phila. W. B. Saunders' Co. 1921.

HOSKINS, H. G. The Tides of Life. The Endocrine Glands in Bodily Adjustment. N. Y. W. W. Norton and Co. 1933.

HRDLIČKA, ALĚS. The Skeletal Remains of Early Man. Smithsonian Misc. Publication No. 3033. Vol. 83. 1930.

HYMAN, L. H. A Laboratory Manual of Comparative Vertebrate Anatomy. Chicago. Univ. of Chicago Press. 1922.

IHLE, VAN KAMPEN, NIERSTRASZ, VERSLUYS. Vergleichende Anatomie der Wirbeltiere. Berlin. Springer. 1927.

JACKSON, C. M. Morris' Human Anatomy. Phila. P. Blakiston's Son and Co. 1925.

JORDAN, D. S. Fishes. N. Y. D. Appleton and Co. 1925.

JORDAN, D. S. Manual of the Vertebrate Animals of North-eastern North America. Yonkers, N. Y. World Book Co. 1929.

JORDAN, D. S. American Food and Game Fishes. Doubleday, Page and Co. 1905.

KAPPERS, HUBER, CROSBY. Comparative Anatomy of the Nervous Systems of Vertebrates. London. Macmillan and Co. 1936.

KEANE, A. H., and A. C. HADDON. Man, Past and Present. Cambridge Press. 1920.

KEITH, SIR ARTHUR. New Discoveries Relating to the Antiquity of Man. N. Y. W. W. Norton and Co. 1930.

KEITH, SIR ARTHUR. A History of the Human Body. N. Y. Henry Holt and Co. 1912.

KELLER, OTTO. Die antike tierwelt. Leipzig. Wilhelm Engleman. 1909.

KINGSLEY, J. S. Comparative Anatomy of the Vertebrates. Phila. P. Blakiston's Son and Co. 1926.

KINGSLEY, J. S. The Vertebrate Skeleton. Phila. P. Blakiston's Son and Co. 1925.

KNOWLTON and RIDGEWAY. Birds of the World. N. Y. Henry Holt and Co. 1909.

KYLE, HARRY M. The Biology of Fishes. N. Y. Macmillan Co. 1926.

LeSOUEF, A. S., and HARRY BURRELL. The Wild Animals of Australia. Sidney, Australia. George G. Harrap and Co. 1926.

LOCY, W. A. Biology and Its Makers. N. Y. Henry Holt and Co. 1928.

LOCY, W. A. The Growth of Biology. N. Y. Henry Holt and Co. 1925.

LOCY, W. A. The Main Currents of Zoology. N. Y. Henry Holt and Co. 1918.

LULL, R. S. Organic Evolution. N. Y. Macmillan Co. 1929.

LYDEKKER, RICHARD. Geographic History of Animals. Cambridge Univ. Press. 1896.

MacFARLANE, J. H. Evolution and Distribution of Fishes. London. Macmillan and Co. 1923.

MARTIN, H. N. The Human Body. N. Y. Henry Holt and Co. 1923.

McCURDY, G. G. Early Man. Phila. J. B. Lippincott and Co. 1937.

McMURRICH, J. P. The Development of the Human Body. 7th ed. Phila. P. Blakiston's Son and Co.

MILLER, W. S. The Lung. Springfield, Ill. C. C. Thomas. 1937.

NEAL and RAND. Comparative Anatomy. Phila. P. Blakiston's Son and Co. 1936.

NEWMAN, H. H. Vertebrate Zoology. N. Y. Macmillan Co. 1920.

NOBLE, J. K. The Biology of the Amphibia. N. Y. McGraw-Hill Book Co. 1931.

NORDENSKIOLD, ERICK. The History of Biology. N. Y. Tudor Pub. Co. 1935.

OBERMAIER, HUGO. Fossil Man in Spain. New Haven. Yale Univ. Press. 1924.

OSBORN, H. F. The Origin and Evolution of Life. N. Y. Charles Scribner's Sons. 1917.

PARKER and HASWELL. Textbook of Zoology. London. Macmillan and Co. 1928.

PATTEN, W. The Evolution of Vertebrates and their Kin. Phila. P. Blakiston's Son and Co. 1912.

PEATTIE, D. C. Green Laurels. Lives and Achievements of Great Naturalists. N. Y. Simon and Schuster. 1936.

PLATE, L. Allgemeine Zoologie und Abstammungslehre. Jena. G. Fischer. 1922.

PRATT, H. S. Manual of the Vertebrates of the U. S. Phila. P. Blakiston's Son and Co. 1923.

RANSON, S. W. The Anatomy of the Nervous System. Phila. W. B. Saunders' Co. 1928.

REYNOLDS, S. H. The Vertebrate Skeleton. London. Cambridge Univ. Press. 1913.

ROMER, A. S. Man and the Vertebrates. Univ. of Chicago Press. 1933.

ROMER, A. S. Vertebrate Paleontology. Univ. of Chicago Press. 1933.

SCHIMKEWITSCH, W. Lehrbuch der vergleichenden Anatomie der Wirbeltiere. Stuttgart. E. Schweizerbart'sche Verlagsbuchhandlung. 1921.

INDEX

Also see Glossary.   Asterisk indicates illustration.

455

DATE OF ISSUE

This book must be returned within 3/7/14 days of its issue. A fine of ONE ANNA per day will be charged if the book overdue.